Exotic invaders in boreal lakes

Assessing impact on biodiversity and ecosystem functioning

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Cover: Macrophyte assemblage, with *Elodea canadensis* in the middle
(K. Tattersdill)

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Exotic invaders in boreal lakes – Assessing impact on biodiversity and ecosystem functioning

Abstract

Invasive species are spreading across the globe, putting pressure on habitats, biodiversity, and key ecosystem processes underpinning ecosystem services. The development of reliable and cost-effective management strategies for these species depends on on-going assessment to justify choices and mitigation initiatives. The invasive macrophyte, *Elodea canadensis* Michx., is one such invasive species spreading deeper into the boreal region of Scandinavia. I aimed to identify a set of traits that contribute to the success of *E. canadensis* in Swedish boreal lakes and investigate impacts on biodiversity (macrophyte and macroinvertebrates assemblages) and ecosystem functions (biofilm metabolism, leaf litter decomposition and nutrient uptake). I achieved this through field studies in six boreal lakes (three invaded by *E. canadensis*), together with a mesocosm experiment. In the experiment, I varied macrophyte diversity and the relative abundance of two invasive macrophytes and quantified macrophyte productivity and nutrient uptake after a drought treatment. In the field, I found that *E. canadensis* started regrowing earlier in the spring than native species. The invasive macrophyte also grew faster as density of its conspecifics increased. Diversity composition of both macrophytes and macroinvertebrates inhabiting the macrophytes differed between invaded and uninvaded lakes. Multiple aspects of ecosystem functioning differed between invaded and uninvaded lakes. The biomass accrual, gross primary productivity of respiration of biofilms, and rates of leaf decomposition were all elevated in invaded lakes, as was entrapment of particulate organic matter. Biofilms were overall nitrogen limited, but nutrient limitation was lower in the invaded than uninvaded lakes. In the mesocosm experiment I found that positive effects of macrophyte diversity on productivity and nutrient uptake decreased as the number of invasive species increased, with only limited evidence that the invasive species altered the impacts of drought.

Although *E. canadensis* is a well-established invasive species, it still impacts biodiversity and functioning in boreal lake ecosystems. In combination with its potential to spread further north, highlights the need to prioritise this and other similar species in management.

Keywords: Elodea canadensis, invasive, macrophyte, growth morphology, biofilm functioning, decomposition, mesocosm experiment, nutrient uptake, community structure

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Främmande arter i boreala sjöar – Att bedöma påverkan på biodiversitet och ekosystemfunktioner

Sammenfattning

Invasiva arter sprider sig på global skala och sätter press på habitat, biodiversitet och centrala ekosystemprocesser som ligger till grund för ekosystemtjänster. Utvecklingen av pålitliga och kostnadseffektiva strategier för att hantera dessa arter är beroende av fortlöpande bedömningar för att säkerställa att rätt val och åtgärder vidtas. Den invasiva makrofyten, *Elodea canadensis* Michx., är en sådan invasiv art som sprider sig djupare in i den boreala regionen av Skandinavien. Mitt mål var att identifiera en grupp av egenskaper som bidrar till framgången för *E. canadensis* i svenska boreala sjöar, och undersöka påverkan på biodiversitet (makrofyt- och makroevertebrat-sammansättning) och ekosystemfunktioner (biofilm, nedbrytning av lövförna och näringsupptag). Jag uppnådde detta genom fältstudier i sex boreala sjöar (tre invaderade av *E. canadensis*), tillsammans med ett mesokosm-experiment. I mesokosm-experimentet varierade jag makrofytdiversiteten och den relativa abundansen av två invasiva makrofyter och kvantifierade makrofyternas produktivitet och näringsupptag efter dom blev utsatt för torka. I mesokosm-experimentet fann jag att den positiva effekten av makrofyt-diversiteten på produktivitet och näringsupptag minskade när antalet invasiva arter ökade. Torka minskade produktiviteten men ökade näringsupptaget i alla mesokosmer. I fält fann jag att *E. canadensis* började återväxa tidigare på våren än inhemska arter. Den invasiva makrofyten växte också snabbare när densiteten av dess artfränder ökade. Makrofytdiversiteten och makroevertebrater som bebor makrofyterna varierade mellan invaderade sjöar och ej invaderade referenssjöar. Flera aspekter av ekosystemets funktion varierade mellan invaderade och ej invaderade sjöar. Det fanns också en tendens till mer partikulärt organiskt material fångat bland makrofyterna i invaderade sjöar. Tillväxten av biomassa, bruttoprimärproduktiviteten och respirationen hos biofilmer, samt hastigheten i nedbrytningen av lövförna var alla högre i de invaderade sjöarna. Biofilmerna var genomgående kvävebegränsade, men näringsbegränsningen var lägre i de invaderade sjöarna än i de sjöar som inte var invaderade.

Trots att *E. canadensis* är en väl etablerad invasiv art, visar den fortfarande påverkan på biodiversitet och ekosystemfunktion i boreala sjöar. Detta, i kombination med dess potential för rörelse och etablering längre norrut, gör att arten bör förbli en prioritet för förvaltning.

Nyckelord: Elodea canadensis, vattenpest, invasiv, makrofyt, växtmorfologi, biofilm, nedbrytning, mesokosmexperiment, näringsupptag, samhällsstruktur

Betre bydi du ber´kje i bakken enn mannavit mykje. Dér betre enn gull i framand gard; vit er vesalmanns trøyst
Håvamål, vers 10

(You will never carry a better burden than good wisdom. It is better than gold on foreign land; wit is a poor mans comfort)

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Tattersdill, K.*, Ecke, F., Frainer, A., M^{c}Kie, B. G. (2017). A head start for an invasive species in a strongly seasonal environment? Growth of *Elodea canadensis* in boreal lakes. *Aquatic invasions,* 12 (4), pp. 487-498.

II Tattersdill, K., Ecke, F., Frainer, A., Angeler, D. G., Bundschuh, M., M^{c}Kie, B. G. Effects of *Elodea canadensis* on ecosystem structure and functioning in boreal lakes (manuscript)

III M^{c}Kie, B. G., Tattersdill, K., Ecke, F., Frainer, A., Sponseller, R. A long-established invasive species alters ecosystem functioning: *Elodea canadensis* and the nutrient limitation of benthic biofilms in boreal lakes (manuscript)

IV Tattersdill, K., Ecke, F., Frainer, A., Angeler, D. G., M^{c}Kie, B. G. Effects of drought and presence of invasive species on macrophyte fragment survival and nutrient uptake (manuscript)

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The contribution of Kristina Tattersdill to the papers included in this thesis was as follows:

I Planned the study together with the co-authors. Carried out the selection of the study sites, sampling, inventory, field experiment and lab work. Had the main responsibility for data handling, data analysis, interpretations, writing and publishing

II Planned the study together with the co-authors. Carried out the selection of the study sites, sampling, inventory, field experiment and lab work. Had the main responsibility for data handling, data analysis, interpretations and writing the manuscript

III Planned the study together with the co-authors. Carried out the selection of the study sites, sampling, field experiment and lab work. Had the main responsibility for data handling. Contributed to data analysis, interpretations and writing the manuscript

IV Planned the experimental study together with the co-authors. Carried out the experiment and associated lab work. Had the main responsibility for data handling, data analysis, interpretations and writing the manuscript

Additional papers

In addition to the papers included in this thesis, the author has contributed to the following papers:

I Bjelke, U.*, Boberg, J., Oliva, J., Tattersdill, K., M^{c}Kie, B. G. (2016) Dieback of riparian alder caused by the invasive *Phytophthora alni* complex: projected consequences for stream ecosystems. *Freshwater Biology* ,61 pp. 565–579

II Stephan, J. G., Pourazari, F., Tattersdill, K., Kobayashi, T., Nishizawa, K., De Long, J. R.* (2017) Long-term deer exclosure alters soil properties, plant traits, understory plant community and insect herbivory, but not the functional relationship among them. *Oecologia* 184(3) pp.685-699

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Abbreviations

AFDM	Ash Free Dry Mass
ANOSIM	Analysis of Similarities
ANOVA	ANalysis Of Variance
DW	Dry Weight
GPP	Gross Primary Production
LME	Linear Mix Effect model
MEM	Mixed Effect Model
N	Nitrogen
NDS	Nutrient Diffusing Substrate
nMDS	non-metric MultiDimensional Scaling ordination
NPP	Net Primary Production
P	Phosphorous
PO_4^{3-}	Phosphate
POM	Particulate Organic Matter
SIMPER	SIMilarity PERcentage analysis
SO_4^{2-}	Sulphate
TIN	Total Inorganic Nitrogen
TOC	Total Organic Carbon

1 Introduction

Humans have a larger impact on the planet than any other single living species (Vitousek, 1994). Our activities are also increasingly facilitating the spread of non-indigenous species (NIS) beyond their native range (Kolar & Lodge, 2001). Travel and trade open up pathways for exotic species to spread, both intentionally (e.g. for agriculture, gardening, fishing stocks) and unintentionally (e.g. through food, crops and soil transportation, together with ballast water) (Levine & D'Antonio, 2003). Anthropogenic disturbances further facilitate establishment of non-indigenous species, e.g. by creating environmental conditions unsuitable for native species. The number of successful species invasions is accelerating (Vitousek *et al.*, 1996), but this is just the tip of the iceberg compared to the total number of species being moved outside of their native range worldwide (Williamson & Fitter, 1996a).

Species invasions often alter the species evenness in the invaded communities in the short run, but can lead to extinctions in the long run (Chapin *et al.*, 2000). These changes to biodiversity are linked to the high biomasses typically attained by invasive species, favouring dominance of habitat and resource use. (Yelenik *et al.,* 2004; Hladyz *et al.*, 2011). However, such extreme levels of dominance by invasive species often occur cyclically or transiently (Simberloff and Gibbons 2004, Strayer et al. 2006), and so the knock-on effects on ecosystem functions may also change over time (Strayer, 2012). Impacts by non-indigenous species may also affect important economic services. Economic impacts may arise from the direct costs of the damage that exotic invaders have on ecosystem services, or potential cost of NIS/ecosystem service mitigation. Hence there are two categories of impact of invasion; ecological and economical, both commonly occurring together, and often interlinked (Mack *et al.*, 2000; Vila *et al.*, 2010). However, the limited quantification of the ecological impacts of invasive species often hinders realistic estimations of economic costs, and setting management priorities (Marbuah *et al.*, 2014)

1.1 What makes a non-native species invasive?

The problem of identifying species properties that are most likely to make NIS become invasive has long been an important topic within invasion biology, especially given some of these traits are also likely to regulate the impacts of invasive species on ecosystem functioning and services. Within invasion biology there are three approaches for predicting what makes certain species become invasive. These work either from the perspective of the invader, of the invaded environment, or a combination of both (Heger & Trepl, 2003). Exemplifying the first approach, Baker (1975) initiated the work by determining properties of the ”perfect weed” which include opportunism, a high degree of adaptability, rapid growth and reproduction. These reflect traits which are likely to serve as assets for invasive species as they spread, along with additional traits that characterise many, but not all, invasive species, such as a large native range and early sexual maturity (Lodge, 1993; Ricciardi & Rasmussen, 1998). There have further been attempts to compare and contrast between invasive NIS and native species as well as NIS that have not become fully invasive (e.g. Williamson & Fitter, 1996b), and comparison of NIS in their exotic and native range (e.g Thiebaut, 2006), However, these comparisons have not presented us with straightforward answers. Commonly, certain NIS have specific characteristics that are important for accomplishing establishment, including effective vegetative/generative reproduction and broad ecological amplitude (Heger & Trepl, 2003). However, Heger and Trepl (2003) found that no invasive plant species had all the invasive properties mentioned, but they still dominated their habitat. Hence, there must be other important factors determining invasion potential, including properties of the invaded ecosystem itself.

The second broad approach to investigating species invasions has been from the perspective of the invaded ecosystem. Dating back at least to Elton (1958), it has been hypothesised that more species rich ecosystems have a greater chance of withstanding invasion, due to the lower chance of an invasive species finding a vacant niche (Chapin *et al.*, 2000). This is based on an assumption that niche availability is a necessary precondition to successful invasion. However, there are also indications to the contrary, where high habitat heterogeneity favours species richness, including invasive species, without an obvious vacant niche being available (Davies *et al.*, 2005). This concept may also include species specific effects, where keystone species facilitate species richness and prevent invasion, or on the contrary act as a strong facilitator making the diverse system more prone for invasion (Palmer & Maurer, 1997). Ultimately, conditions that determine biodiversity (e.g. environmental conditions, competition, stress and disturbance) might often also strongly regulate invasiveness (Levine & D'Antonio, 1999; MacDougall & Turkington, 2005). Furthermore, invasive species are particularly favoured by a combination of high resource availability in the system together with its adaptation to high resource utility and lack of enemies/herbivores in the recipient area (Blumenthal, 2005, 2006). This indicates that when environmental conditions for the NIS are favourable, the invasive pressure on the ecosystem is potentially large (Davis et al., 2000; Richardson & Pysek, 2006).

1.2 Species invasion: Impact on biodiversity and ecosystem functioning

Truly invasive species often have strong, ecosystem-level impacts, from local to landscape scales. These impacts can be seen in effects on not only ecosystem structural parameters, such as ecosystem architecture, biodiversity, and food-web configurations, but also on ecosystem functioning. The impacts of invasive species on biodiversity have been given large attention over the decades (Lodge, 1993; Pimm *et al.*, 1995; Levine & D'Antonio, 1999). Invasive species are highly competitive (Blossey & Notzold, 1995; Vila *et al.*, 2010) and can be the direct cause of extinction of rare species (Elton, 1958; Pimm *et al.*, 1995). This has potentially profound consequences for biodiversity and species interactions (Chapin *et al.*, 2000). Occasionally establishment of exotic species may not bring about any species extinction, and its presence may thus increase net biodiversity (Vermeij, 1991). However, the relative abundance between species (evenness) over time may change, and therefore exotic species can still reduce biodiversity, even without reducing species numbers (Chapin *et al.*, 2000). The effect of exotic invaders on biodiversity is thus always linked to the functional attributes of all species in the system, and hence if biodiversity changes then ecosystem functioning will likely also be altered (Figure 1; Chapin *et al.*, 2000; Hooper *et al.*, 2005).

Invasive species often reach high biomass (Lodge, 1993) and have unique attributes that may impact the habitat structure in the first instance. The impact of invasive foundation species (e.g. macrophytes) or ecosystem engineers (e.g. crayfish and zebra mussel) are often particularly marked, since such species define the habitat and thus impact the abiotic and biotic attribute of the system (Strayer, 2010). Consequently, ecosystem functioning may shift because of changes in habitat configurations, or as a result of other activities of the invasive species within the ecosystem. These include impacts on primary production (zebra mussel; (Vanderploeg *et al.*, 2002), or the decomposition of organic matter (Hladyz *et al.*, 2011)). Such effects may be positive, in cases where the presence of the species increases functional diversity, such as when zebra mussels filter the water column and move the nutrients to a benthic system (Goedkoop *et al.*, 2011), or negative if it decreases functional diversity and changes the habitat characteristics (Horgan *et al.*, 2014).

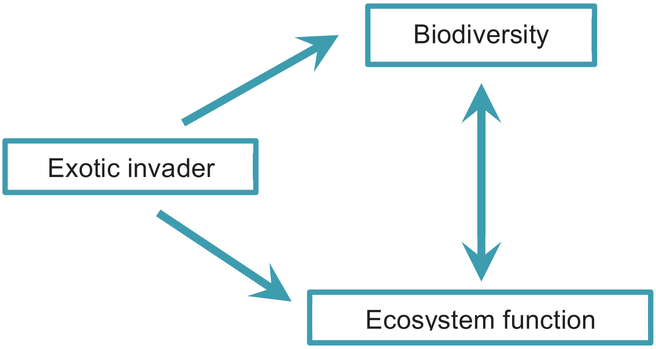


Figure 1. The impact of an exotic invader on biodiversity and ecosystem function

1.3 Invasive species in freshwater habitats

Freshwater covers only 0.8 % of the Earth's surface, but is of fundamental importance for human populations. The usage of fresh water by humans is arguably more extensive than any other natural resource: for drinking water, wastewater and food capture/production, and energy production. With this immense pressure on freshwater comes also large threats to freshwater habitats and biodiversity. Significantly, species invasions were put forward as one of 5 main threats to the integrity of freshwater habitats by Dudgeon et al. (2006), along with overexploitation, water pollution, flow modification and habitat degradation. Along similar lines, land use change and invasion by non-native species are both seen as the two major threats to freshwater environments in the 21st century (Allan & Flecker, 1993; Sala *et al.*, 2000), already impacting biodiversity (Ricciardi & Rasmussen, 1999; Dudgeon *et al.*, 2006).

As a generalization, water bodies may be less variable in their environmental features than land habitats, favouring widespread establishment of NIS once in a region (Cook, 1985). The large connectivity of water bodies means that NIS entering a freshwater catchment may rapidly be transported through the river network. Like ballast water it may travel far and increase invasion pressure on recipient waters (Ricciardi & Rasmussen, 1998). Invasive freshwater organisms can be introduced via ballast water, or as part of the horticultural and aquarium industries (García-Berthou *et al.*, 2005; Hulme, 2009). The high probability of reintroduction events and the high amount of individuals per introduction event increases the genetic diversity of introduced species (Roman & Darling, 2007). The human pressure on freshwater ecosystems makes them vulnerable and prone to disturbance, further increasing the probability of successful establishment for invasive freshwater species (Sala *et al.*, 2000; Didham *et al.*, 2005). Freshwater invasive species are particularly successful at adapting to the environmental conditions they encounter as they spread into new habitats, as exemplified by invasive macrophytes (Riis *et al.*, 2010; Tattersdill *et al.,* 2017).

1.3.1 Macrophytes

Macrophytes are an important group of primary producers in freshwater habitats, but some species are also among the most important freshwater invasive species globally (Chambers *et al.*, 2008). Broadly, macrophytes are grouped into submerged (elodeids and isoetids), emergent (helophytes) and floating life forms (nymphaeids and lemnides), of which the fully submerged macrophytes are particularly important in regulating nutrient cycles at both within-lake and landscape scales (Schindler & Scheuerell, 2002; Williamson *et al.*, 2008) (Figure 2). Submerged macrophytes, although rooted, take most of their required nutrients from the water (Madsen & Cedergreen, 2002; Christiansen *et al.*, 2016). Indeed, the presence of a well-developed and diverse community of submerged macrophytes is often synonymous with high levels of water transparency in lakes (eg. (Moss *et al.*, 1996). However, the role of macrophyte diversity per se in regulating rates of nutrient removal and the stability of nutrient cycling in lakes remains limited.

Submerged macrophytes are a fundamental component of the biodiversity and ecosystem functioning of lakes, having many attributes of foundation species (Angelini *et al.*, 2011). They contribute to lake primary productivity, and their uptake of nutrients, coupled with the presence of dead plant material are key components of lake nutrient and carbon cycling, and oxygen dynamics (Ozimek *et al.*, 1993; Van Donk *et al.,* 1993; Jeppesen *et al.,* 1998). Submerged macrophytes are also morphologically diverse, providing food and/or shelter for fish, mammals, birds and marcoinvertebrates (Jeppesen *et al.,* 1998). Submerged macrophytes typically spread through vegetative propagules. Fragments are generated and transported through wave action, herbivory, boat motors and other anthropogenic disturbances (Mack *et al.*, 2000; Kelly & Hawes, 2005; Riis & Sand-Jensen, 2006). Some plants also actively self fragment (e.g. *Myriophyllum spicatum*) (Xie & Yu, 2011). The survival potential of most fragments is high (Riis, 2008), and so they contribute to the primary production in the freshwater habitat and the uptake of nutrients from the water column. However, floating fragments may drift on to land where they are exposed to desiccation, which have further impact on species survival and establishment (Barrat-Segretain & Cellot, 2007; Riis, 2008).

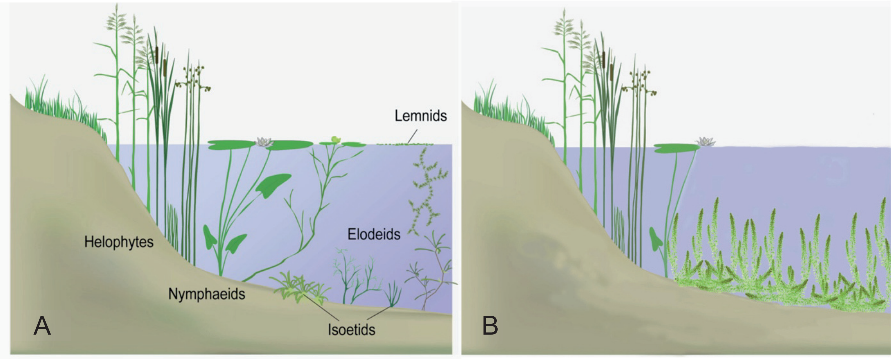


Figure 2. Growth forms in the macrophyte bed in the littoral zone of an uninvaded lake (A) and a macrophyte bed invaded by the submerged Elodeid *"E. canadensis* (B) (Ecke, F. & Vnuk, M. after Andersson (1999); figure B is a modification of A)

Vegetative fragmentation is an important mode of spread also for invasive macrophytes. As with other freshwater habitats, macrophyte beds are prone to invasion by non-native species. In line with aquatic invasive species, a major vector for introduction of new non-native macrophytes is the aquarium and gardenpond trade, after which they find their way into rivers and lakes (Hussner *et al.*, 2010). Invasive macrophytes typically have multiple weed-like properties, including high growth rates, early seasonal growth, and broad environmental tolerances, which further facilitate their rapid expansion, and often give them advantages over native species (Williamson & Fitter, 1996b). Invasive macrophytes may reach very high biomass at local scales, with strong impacts on habitat complexity, community structure, ecosystem functioning (Schultz & Dibble, 2011; Alnoee *et al.*, 2016), and on ecosystem services and economic activity (Marbuah *et al.*, 2014). One such invasive species that establishes in boreal lake littoral habitats is the invasive elodeid *Elodea canadensis* Michx. It is native in North America but was first observed in England in 1836, and reaching Sweden in 1874 (Josefsson & Andersson, 2001). It has a large distribution within Europe (Hussner, 2012), and is the focal species for my research.

1.3.2 *Elodea canadensis* (Canadian waterweed)

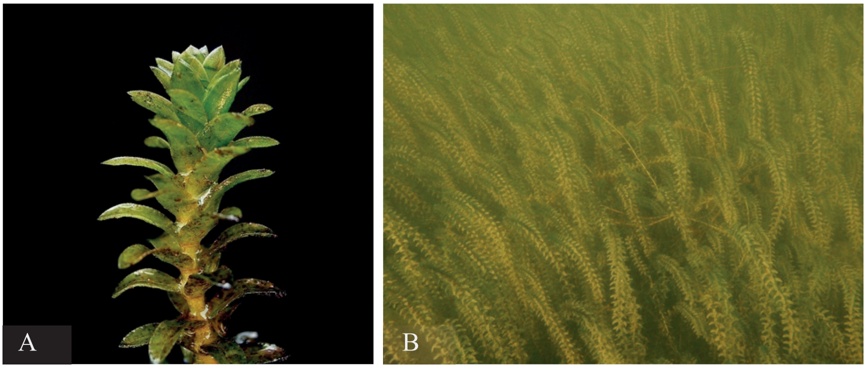


Figure 3. *Elodea canadensis*, singular plant (a) (Wikimedia commons) and large stand in Lake Lötsjön, Sweden, 2013 (b) (Photo: K.Tattersdill)

Elodea canadensis Michx. is a submerged macrophyte that forms dense stands with plants reaching the water surface in optimal conditions (Cook & Urmikonig, 1985; Mjelde *et al.*, 2012) (Figure 3b). It has been observed that *E canadensis* populations go through a typical boom and bust cycle (Simpson, 1984; Rørslett *et al.*, 1986; Simberloff & Gibbons, 2004). This cycle may involve several years where the species is present at low abundances, prior to a sudden great population expansion. Following this, a population collapse occurs, and then the population may either establish itself at an equilibrium level, or the boom and bust cycle may commence again (Simberloff & Gibbons, 2004). Population expansion is through spread of vegetative fragments (Cook & Urmikonig, 1985). The fragments can establish in a broad environmental range, but the plant prefers fine sediment with some organic material (Pearsall, 1920; Nichols & Shaw, 1986), and nutrient rich, alkaline lakes and slow flowing rivers (Nichols & Shaw, 1986; Blanchet *et al.*, 2012). However, *E. canadensis* is highly tolerant to a large variation of nitrogen concentrations and C:N ratio (Blanchet *et al.*, 2012), and has no strong preference for phosphorus source (Eugelink, 1998). Nonetheless, the macrophyte species is good at reducing nutrient loads in nutrient-rich lake water (Ozimek *et al.*, 1993; Ciurli *et al.*, 2009; XiaoXia *et al.*, 2013), as it takes most of the required nutrients from the water column (Madsen & Cedergreen, 2002; Christiansen *et al.*, 2016). *Elodea canadensis* is also highly tolerant of a wide range of temperatures (Cook & Urmikonig, 1985; Nichols & Shaw, 1986), where the whole plant may overwinter under the ice (Stuckey *et al.*, 1978). However, it might also die back and regrow in early spring from dormant apices (Stuckey *et al.*, 1978; Tattersdill *et al.,* 2017).

Several key attributes of *E. canadensis* are likely to be crucial for understanding its impacts on biodiversity. For example, the combination of broad environmental tolerances and high adaptability, efficient growth and ability for vegetative fragmentation makes *E. canadensis* an aggressive invasive species (Cook & Urmi-König, 1985). The capacity to use bicarbonate as a C source in photosynthesis lets it operate effectively even during shortages of CO_2, increasing its competitive advantage (Sand-Jensen & Gordon, 1986). Furthermore, it has been shown that *E. canadensis* produces allelopathic chemicals that reduce growth of periphyton (Erhard & Gross, 2006; Hu & Hong, 2008). All these attributes contribute to the capacity of *E. canadensis* to form dense stands. Indeed, *E. canadensis* appears to grow somewhat better when it was with its conspecifics (Barrat-Segretain, 2005). In these dense stands, *E. canadensis* shade out and outcompetes native macrophyte species and alter their relative abundance (Rørslett *et al.*, 1986; Mjelde *et al.*, 2012). The presence of the invasive macrophyte has also been seen to alter the composition of invertebrates and fish utilising this habitat (Kelly & Hawes, 2005; Kornijów *et al.*, 2005).

Aspects of ecosystem functioning are also likely to be impacted by invasion by *E. canadensis*. For example large stands of *E. canadensis* absorb enough nutrients from the water column to suppress algal blooms (Rørslett *et al.*, 1986). The submerged macrophyte can additionally retrieve nutrients and contaminants via the roots from sediment and later, through decomposing plant material, release it to the water column (Jackson *et al.*, 1991). The roots may also stabilize the sediment, at least at large plant densities (Schultz & Dibble, 2011), however, the above ground biomass could obstruct water current (Sand-Jensen, 1998). Changes in the light, nutrient and pH environment might also affect the functioning of biofilms growing on organic and inorganic substrates within the macrophyte bed (Jones *et al.*, 1999; Gette-Bouvarot *et al.*, 2015; Mora-Gómez *et al.,* 2016). These biofilms include auto- and heterotrophic microorganisms (algae, bacteria, fungi) that play a key role in absorbing nutrients from the water column (Battin *et al.,* 2016, Mora-Gómez *et al.,* 2016). The environmental effects of *E. canadensis*, along with any changes in composition of invertebrates might similarly be expected to affect processes of organic matter decomposition. Leaf litter decomposition is a key process integrating terrestrial matter into the aquatic food web (Gessner & Chauvet, 2002). This can be mediated by microorganisms that use leaf litter as a substrate and detritivores using both leaf material and microbes as food resource (Wallace & Webster, 1996; Gulis & Suberkropp, 2003).

1.4 Evaluating risks requires empirical knowledge

The level of risk and impact imposed by an invasive species is likely to vary regionally, according to characteristics of the native biota, degree of human impact and longer-term history of invasion, among other factors (Schirmel *et al.*, 2016). This points towards the need for local and ongoing assessments of a given species. It is important that such assessments do not only consider impacts on the particular organism group from which a given invasive species comes (e.g. macrophytes in the case of *E. canadensis*). Rather, risk assessments for invasive species should also consider impacts on other biota associated with that organism group and further the knock-on effects this might have on ecosystem functioning (Sousa *et al.*, 2011; Strayer, 2012). These assessments should also consider species which may have been long-established in a region but which may (i) still be having an impact in that region and (ii) have ongoing potential to spread beyond that region (Jeschke *et al.*, 2014). In my research, I have focused on *E. canadensis* as a model invasive macrophyte, with additional research conducted on the closely related and currently highly invasive *Elodea nuttallii*. In common with other invasive macrophytes, both these species reproduce readily, spread rapidly, and have multiple impacts on habitat architecture, I assessed whether *Elodea canadensis*, long established in Sweden, continues to have impacts on biodiversity and ecosystem functioning. Ultimately, my goal was to generate data and knowledge that can contribute to an evidence-based assessment of the ongoing risk posed by *E. canadensis*, and other similar macrophytes, to boreal lake ecosystems.

2 Overall aim of the study

The overarching aims of this study were to identify a set of traits that contribute to the success of *Elodea canadensis*, a model invasive macrophyte, in Swedish boreal lakes and investigate impacts on biodiversity (macrophyte and macroinvertebrates assemblages) and ecosystem functions (biofilm, leaf litter decomposition and nutrient uptake).

These aims are addressed in the four different papers

Paper I – Quantify key abiotic and biotic variables regulating *E. canadensis* propagule establishment and growth, and compare the performance of propagules established in August *vs* November the following spring, focussing on their growth and morphology

Paper II – Assess how *E. canadensis* affect macrophyte diversity, macroinvertebrates associated with macrophytes, accumulation of particulate organic matter and the key ecosystem process of leaf litter decomposition

Paper III – Consider how the presence of *E. canadensis* affects the growth and metabolism of benthic biofilms, with a focus on how the plant affects nutrient limitations of biofilm activity

Paper IV – Investigate how the diversity (encompassing both species richness and evenness) of two native and two invasive species of macrophytes regulates the impacts of a drought stressor on two ecosystem processes: macrophyte productivity and nutrient uptake

3 Method

My research consisted of three main components, which differed in study systems and methodology, though there was some overlap also.

Component 1 – field sampling and inventories to establish background information on water chemistry variables, coverage of *E. canadensis* and other macrophyte species, and data on macroinvertebrates living on the macrophytes (Paper I-II)

Component II – field experiments including investigations of the growth of *E. canadensis* propagules, leaf litter decomposition and nutrient limitation of biofilms (using nutrient diffusing substrates) (Paper I-III)

Component III – a mesocosom experiment, looking into effects of invasive species richness and abundance on the ecosystem processes of macrophyte productivity and nutrient uptake (Paper IV)

Together, theses components complemented one another in quantifying *E. canadensis* attributes and effects on biodiversity and ecosystem function (Figure 4)

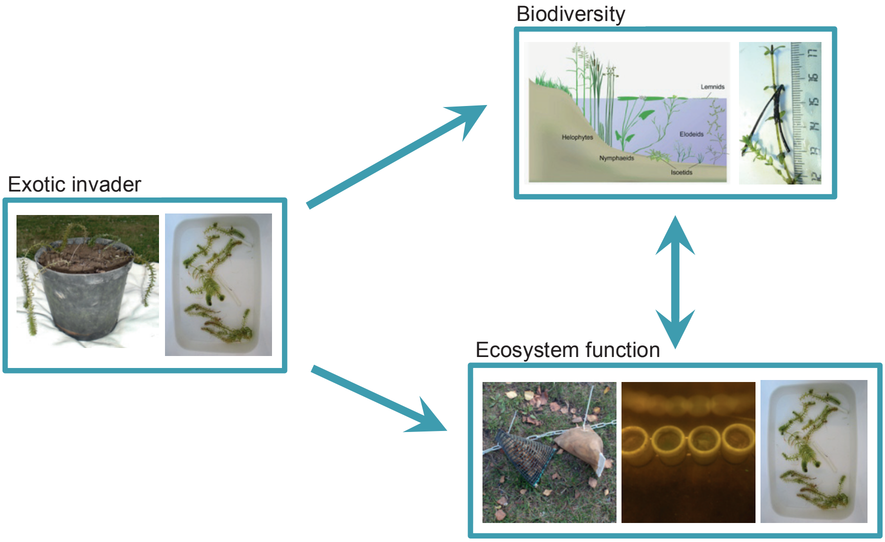


Figure 4. The different components of the field and lab sampling campaign and experiment. Information on exotic invader (*E. canadensis*) through: growth experiment and mesocosm experiment; Biodiversity: macrophyte inventory, and macroinvertebrate sampling on macrophytes; Ecosystem function: leaf litter decomposition, nutrient uptake (both in the field and lab experiment) and macrophyte productivity.

3.1 Field study sites (paper I – III)

Study systems for the field study comprised six lakes, three invaded by *E. canadensis* (Lake Lötsjön, Lake Sparren and Lake Ubby långsjön), and three uninvaded reference lakes (Lake Långsjön, Lake Ruggen and Lake Ströjan, absence of *E. canadensis*), all situated in Uppland, Sweden (Figure 5). Three transects per lake were chosen based on the presence of submerged macrophytes, separated from other similar bays by intervening areas of *Phragmites* sp. The invaded lake transects were chosen based on the presence of *E. canadensis*. *Elodea canadensis* was absent from the univaded lakes, but I checked there was still a mixed native assemblage including typical genera such as *Myriophyllum* spp. The macrophyte inventory defined the area covered by the transects (see paper II). The fieldwork was conducted between August 2013 and September 2014 (Figure 6). All sampling and experiments were analysed at lake transect level.

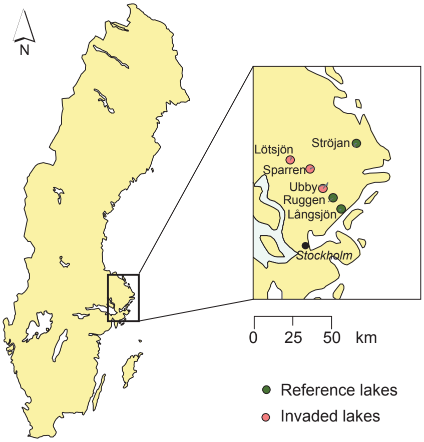


Figure 5. Map of Sweden with the chosen lakes for field study situated in Uppland; three reference lakes (green) and three lakes invaded by *E. canadensis* (pink)

3.2 Component I – Field sampling (paper I – III)

3.2.1 Water sampling (paper I – III)

Water samples were taken for chemical analyses at each lake transect within the six lakes once during August 2013, beginning of May 2014 and before and after the nutrient diffusion substrate experiment conducted in August 2014 (Figure 6). Secchi depth was measured in August 2013 and 2014 in every lake using a Secchi disc (diameter, 30 cm). Temperature, oxygen concentration and turbidity were measured on site using a Manta^{TM} multiprobe (Eureka Water Probes, Austin TX). The water samples were analysed at the Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences (SLU) following international (ISO) or European (EN) standards (Fölster *et al.*, 2014 and references therein). Specific analytical methods are given in the supplementary material in Tattersdill *et al*. (2017).

3.2.2 Macrophyte inventory (paper I and II)

Two macrophyte inventories were conducted to identify macrophyte presence and coverage (%) across the selected transects in all six lakes. The first was completed during August 2013. It consisted of inventorying a 5 m stretch perpendicular to the beach reaching a depth of around 115 cm (meaning that the transects varied in size due to transect profile (see paper II). The second was conducted at the end of March 2014 to characterise the occurrence of *E. canadensis* early in the season relative to native species in the defined lake transects, based on presence/absence in a 0.25 m narrow transect within the main transect.

3.2.3 Macroinvertebrate sampling (paper II)

Macroinvertebrates associated with macrophytes were sampled with a 25 x 25 cm net (0.5 mm, wholes) placed over the macrophytes. The macrophytes enclosed within the net were cut at the base of the plants. Three samples were taken per transect in all six lakes. Samples were washed over a sieve (0.5 mm) to collect macroinvertebrates and particulate organic matter (POM). Macroinvertebrates were identified mostly to species level, and stored in 70 % ethanol. Macrophytes were sorted by species and dried and weighted for dry weight determination. Organic material was sorted into larger fractions (twigs, cones, leaves) and particulate organic matter (larger than 0.5 mm)

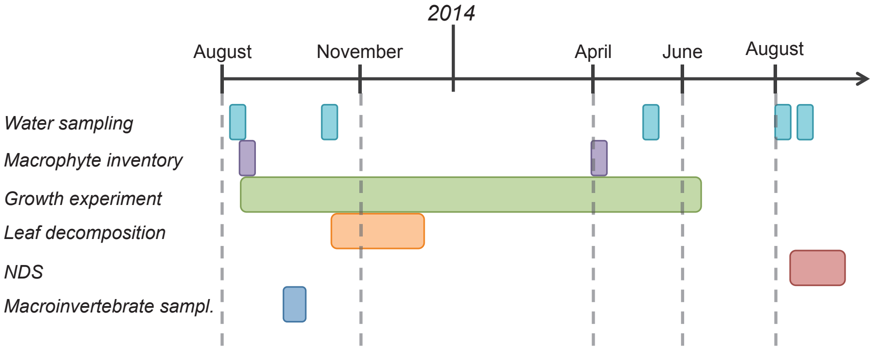


Figure 6. Time line showing when sampling and field experiments were conducted during the period between August 2013 and September 2014. Water chemistry sampling (light blue), macrophyte inventory (purple), growth experiment (green), leaf litter decomposition (orange), NDS (nutrient diffusion substrate, red) and macroinvertebrate sampling (dark blue)

3.3 Component II – Field experiments (paper I – III)

3.3.1 Growth experiment (paper I)

A growth experiment focussed on *E. canadensis* was performed from August 2013 to beginning of June 2014, in the three lakes invaded by *E. canadensis* (Lake Lötsjön, Lake Sparren and Lake Ubby långsjön). This consisted of planting five shoots with apical tips in a pot containing a sand and soil mixture (4:1)(Figure 7a). In total 270 pots were placed out in August and retrieved in mid August (after 2 weeks acclimation period), beginning of September, October, November and then again in the beginning of April and June. Another set of 135 pots were placed out in the selected transects in November 2013, and retrieved two weeks later, and then again at the beginning of April and June. After retrieval different growth parameters were taken and roots and plant material dried separately.

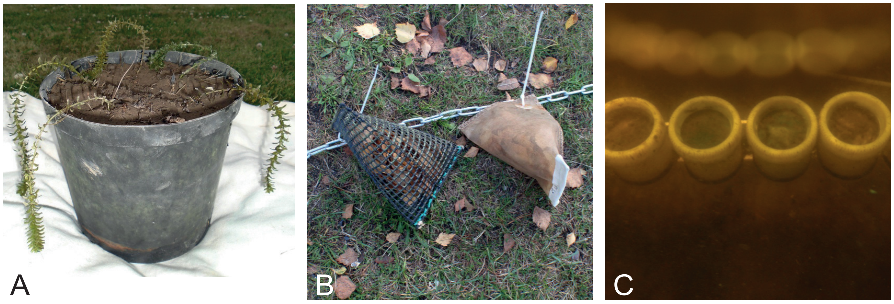


Figure 7. Experimental units; five *E. canadensis* shoots planted in a pot prior to start of the growth experiment (A), leaf litterbags used to study the organic matter decomposition; coarse mesh bag, left and fine mesh bag, right, prior to start (B) and nutrient diffusion substrate jars deployed in a lake-transect, used in the study of biofilm growth and metabolism (C) (Photos by K. Tattersdill)

3.3.2 Leaf litter decomposition

Dried birch leaves, collected at autumn abscission, were placed in coarse and fine mesh bags (Figure 7b, see also Figure 6 for timeline). The coarse mesh size was sufficient to allow access by invertebrate detritivores and shredders. In bags with a fine mesh size access was blocked for invertebrate shredders and only microorganisms would decompose the leaves and thus decomposition was primarily attributable to the activities of microbial organisms alone. Five replicate bags per mesh size were placed along the lake transects in both invaded and uninvaded control lakes. The bags were deployed in the lakes for two months, after which the litter was weighed to determine the decomposition of leaf material. On retrieval leaf bags were frozen. Later, bags were defrosted and leaves washed in a sieve (0.5 mm), Macroinvertebrates from the coarse mesh bags were picked and identified to species level. Leaf discs (diameter 10 mm) were taken for ergosterol determination. Ergosterol is a component of fungal cell walls, and is here quantified as a measure of fungal biomass on the leaf litter. The remaining leaf material was dried and burned for ash free dry mass (AFDM) determination.

3.3.3 Nutrient diffusing substrates (paper III)

I conducted a nutrient diffusing substrate (NDS) experiment to investigate the responses of biofilms to the presence of invasive macrophyte *E. canadensis*. The NDS experiment was conducted in August 2014 in invaded and uninvaded reference lakes (Figure 6). Jars (60 ml) containing control or nutrient spiked (nitrate, phosphorous, or both) 2 % agar gel were used. I also included two different filters, organic birch veneer (thickness 1 mm, diameter 45 mm) and inorganic glass fibre filter (diameter 45 mm, pore size 1 μm, Pall Life Science). Four replicates of each nutrient amendment and corresponding filter was placed in all lake transects (Figure 7c). After 21 days the jars were collected for further analysis of the biofilm colonizing the two different filters. Firstly, the oxygen dynamics of the retrieved biofilms were quantified in the laboratory, with gross primary production (GPP) and respiration measured after 3 hours in light regime or dark regime respectively. Secondly, chlorophyll-a concentration of the biofilm was measured using BenthoTorch (bbe Moldaeanke) and extraction.

3.4 Component III – Mesocosm experiment (paper IV)

I conducted a macrophyte biodiversity-ecosystem functioning experiment in laboratory mesocosms during the summer of 2015. Two invasive species (*E. canandensis* and *E. nuttallii*) and two native species (*Myriophyllum spicatum* and *Ceratophyllum demersum*) were mixed in monocultures or three-species combinations, with 12 plant shoots in total in each mesocosm. The experiment was performed for 21 days with a drought stressor initiated after 7 days lasting for 10 hours. At day 20 a 2 mg/l NO_3-^{15}N isotope was added to all mesocoms, before termination the following day. For each mesocosm, species were separated per species and dried for dry weight determination. Samples were grinded and measured for ^{15}N content.

3.5 Data analyses

Variation in water chemistry variables and additional environmental variables between lake-transects were visualised by performing a principal component analysis (PCA) (paper I), and also by performing a linear mixed model (LME) analysis on the water chemistry variables with lake invasion statys fitted as a fixed factor (paper II).

Macrophyte species coverage and macroinvertebrate species (abundance) between lake-transects was visualized through a non-metric multidimensional scaling ordination (nMDS) (see also paper II). Analysis of Similarities (ANOSIM) was performed on these datasets to assess divergence in community composition between the invaded and control lakes. This was followed by a similarity percentage analysis (SIMPER) to assess which species explained most of this dissimilarity. Variation in macrophyte biomass and POM from the macroinvertebrate samples were analysed using a LME, with lake invasion status fitted as a fixed factor, and lakes and transects nested in lakes fitted as random factors. Macroinvertebrate richness, abundance, Shannon diversity and evenness were also tested using this model, together with a rarefied richness and richness and abundance of macroinvertebrates per gram dry weight of macrophytes.

Different plant variables from the growth experiment were tested against water chemistry and environmental variables PCA axis one and initial *E. canadensis* cover in each lake-transect (%, from the inventory) through a LME analysis (see also paper I). Initial *E. canadensis* cover was used to identify potential intraspecific competition. Establishment periods (August and November) were also compared using a LME. Linear regression was used to compare different plant variables.

Leaf litter decomposition rate per day (see also paper II) was calculated based on initial and final ash free dry mass using the negative exponential model (Benfield 1996); *ln* final AFDM – *ln* initial AFDM)/day and analysed in a mixed model to identify differences between invaded and control lakes and mesh size. Ergosterol, as a measure of fungal biomass, was analysed using the same model. Linear regressions were used to analyse the relationship between decomposition rate in coarse mesh bags and shredder abundance and richness found in the bags.

For the NDS experiment (see also paper III) I used a mixed effect model (MEM) ANOVA to assess responses of biofilm respiration, GPP and chlorophyll-a mass to nutrient addition and between the invaded and control lakes. For each or these responses, I also calculated the nutrient response ratio (NRR) for each of these response variables as the ratio of the value observed for each nutrient treatment (i.e. N, P or N + P) to the control from each replicate group row. An NRR above one for a particular nutrient treatment indicates that that nutrient or nutrient combination is limiting for a given response variable. I also calculated the ratio of GPP:respiration, as a measure of the level of autochthony to allochthony in our biofilms. These models tested the fixed effects of lake invasion status, nutrient treatment and substrate type, with random effects including lake, transects nested within lakes, and blocks (i.e. one group of control, N, P and N + P treated NDS) nested within transects and lakes.

For the mesocosm experiment (paper VI) I also performed a mixed effect model testing the effect of drought stress, species richness, invasive richness and invasive relative abundance on relative biomass ratio (end biomass dry weight – starting biomass dry weight) and ^{15}N uptake. I also applied the Loreau and Hector (2001) diversity effect partition. This partitions the "net diversity effect" (i.e. degree to which the functional yield of a species mixture exceeds expectations based on the performance of species monocultures). The net diversity effect is divided into two fractions: complementarity and the species selection effect. Complementarity quantifies species mixture yields compared to the expected based on their monoculture performance, while the selection effect reflects dominance of species with particular traits that favour higher process rates in multi-species assemblages (Loreau & Hector, 2001; Cardinale *et al.*, 2002; Fox, 2005).

Data was standardized, log- or square root-transformed in all analyses when inspection of residual plots indicated non-normality and heterogeneous variances, to satisfy parametric assumptions. The statistical analyses were performed using R (R-Core Team 2013) and its corresponding packages (see specific papers) and program JMP® Version 10 (SAS Institute Inc., Cary, NC).

4 Results and discussion

My research has revealed new knowledge about the attributes that help explain the success, dynamics and impacts of *Elodea canadensis* in boreal lakes. These insights are crucial for understanding the present impacts of *E. canadensis* in its current range, but also forecasting its potential impacts as it spreads north into sensitive regions, including arctic and northern alpine habitats. Furthermore, given that this species can be regarded as a model species for other invasive macrophyte, my results can also give insights into the potential impacts of multiple invasive plants that are on the verge of entering Sweden (Hallstan, 2005; Naturvårdsverket, 2011). Among my key results are the findings that *E. canadensis* grows best with its conspecifics, is capable of establishing late in the autumn, and can begin regrowing early in the spring (paper I). I also found important impacts on macrophyte community composition, and consequences this have on macroinvertebrate assemblages inhabiting macrophyte beds (paper II). I further found important shifts in ecosystem functions, including changes in litter decomposition and quantities of particulate organic matter, the metabolism of biofilms, and process of macrophyte productivity and nutrient uptake (papers II-IV). This includes important effects on functioning arising from interactions between *E. canadensis* and another invasive species, *E. nuttallii*, as well as native macrophyte species (paper IV). Taken together, my results show that *E. canadensis* has impacts on aspects of biodiversity and ecosystem functioning, that ultimately underpin lake ecosystem stability.

4.1 Attributes of an invasive species

By following *E. canadensis* growth in the field through less known periods of the year (paper I) I could identify attributes that are important for its survival and competition with native species in boreal lakes (Figure 8).

4.1.1 Establishment and Growth

In my plant growth experiment (paper I), *E. canadensis* biomass was linked to high alkalinity and high ambient cover of *E. canadensis*. The latter result indicates it grew more when it was surrounded by its conspecifics. This tendency was also observed during a mesocosm experiment (paper IV) where *E. canadensis* grew better in aggregated assemblages (monoculture and dominating in polycultures). Barrat-Segretain (2005) observed similar results with rooted plants in experimental setup. These results point towards a re-enforcing effect of increased population density on growth. This is in line with the boom and bust theory (see section 1.3.2) where there is a facilitation of growth after a slow initial establishment period (Simberloff & Gibbons, 2004). Such intraspecific facilitation could arise from the ability to control light environment and nutrient availability (Mccreary, 1991; Gaston, 1999; Jiang *et al.*, 2010). *Elodea canadensis* is also known to produce allelopathic chemical to prevent the growth of competitive periphyton (Erhard & Gross, 2006).

Establishment period seem important for macrophyte survival. Thus I used the growth experiment to shed light on two different establishment periods (August and November), through differences in propagule growth. I found that there was no difference in the mean length of new re-growth per shoot, ($F_{(1,137)} = 0.19$, $p = 0.661$ (mean ± SE; 3.1 ± 0.2 cm (August) and 4.0 ± 0.2 cm (November)), indicating that the propagules, despite difference in establishment period, did equally well. I also saw an increase in internode length for the fragments established in November in beginning of April (0.38 ± 0.01 cm) and further in June (0.65 ± 0.04 cm). However, by the time of the sampling point in June there was no difference in internode length to fragments established in August (0.59 ± 0.04 cm).

My spring field survey (paper I) revealed that *E. canadensis* showed signs of regrowth already in early spring (beginning of April), when the water temperature had not exceeded 5°C. These findings, together with the successful growth of the autumn propagules are indicative of an opportunistic growth strategy over native species barely present at the time (paper I). *Elodea canadensis* displays capacity for exploiting available energy in generating growth even when conditions are not favourable. These attributes are likely to give this invasive macrophyte a competitive advantage in strongly seasonal habitats such as boreal lakes

4.1.2 Morphology

The morphology of macrophytes including *E. canadensis* in the littoral zone has a large impact on other organisms that live there. In my growth experiment (paper I), the plant individuals that were larger also tended to have more shoots (R^2 = 0.762, p <0.0001), presenting denser foliage for other organisms to inhabit. Additionally, internode length (measured as distance between leaf-whorls) increased with high ambient *E. canadensis* biomass and high TOC and PO_4. The latter two variables could unfortunately not be separated due to high correlation (R^2 = 0.85). However, this clearly shows that the plant invests in above ground biomass to compete for sunlight as water colour and density increases (also seen by Mielecki & Pieczynska (2005) and Mormul *et al.*, (2012) in experimental settings). These findings add to previous data indicating the high phenotypic plasticity within *E. canadensis* (Riis *et al.*, 2010).

4.1.3 Fragmentation

Vegetative dispersal is an important means of spread for invasive species such as *E. canadensis* (Lockwood *et al.*, 2005; Riis, 2008), which have shown to fragment easily (Cook & Urmi-König, 1985). I observed that the invasive plant produced more fragments when they became larger, increasing the spread potential (R^2 = 0.385, p <0.0001). *Elodea canadensis* has a tendency to fragment more easily than other invasive species (Redekop *et al.*, 2016). At local scales this may reduce its biomass relative to species that fragment less, but at larger scales the production of vegetative propagules in the form of fragments is an important pathway for spread and establishment, and is one of the major attributes to the success of invasive macrophytes (Lockwood *et al.*, 2005).

4.2 Invasive species and effects on biodiversity

Boreal lakes in both Europe and North America are at the northern edge of *E. canadensis* distribution range (Maiz-Tome, 2016). Ongoing global changes may favour its further expansion in this region and beyond, highlighting the urgent need to evaluate the impact on biodiversity in this region (Figure 8).

4.2.1 Macrophyte community

Macrophyte community composition differed between the invaded and uninvaded reference lakes (reflecting in both nMDS and ANOSIM (see paper II)). Most significantly, *Myriophyllum* spp was lacking in most of the invaded lakes' transects studied (except one in Ubby långsjön), which is interesting as these are otherwise common species in central Sweden (Ecke, 2018). A similar negative association has been observed between *E. canadensis* and

Myriophyllum spp. (Mjelde *et al.*, 2012; Grudnik & Germ, 2013). There was also a clear effect on species richness ($F_{(1,4)} = 10.465$, $p = 0.032$), which surprisingly was higher (11.7 ± 1.2) in invaded lakes than in uninvaded reference lakes (6.9 ± 0.8). There was a tendency that the coverage of the macrophytes was larger in the invaded lakes than in the uninvaded lakes ($F_{(1,4)} = 4.604$, $p = 0.098$ (85 ± 11 and 41 ± 6 %, respectively). *Elodea canadensis* have shown based on this study and by other (Larsson & Willén, 2007), that it often prefers heterogeneity in the habitat, increasing niche availability. Caution is needed in interpreting the species richness result, as it may not indicate an overall increase in diversity in the longer term. For example, it is likely that the richness, or alt least the evenness might decrease as the invasive species become more dominant (Rørslett *et al.*, 1986; Strand & Weisner, 2001). Furthermore, any increase in richness should be balanced against the changes in community composition (e.g. exclusion of *Myriophyllum*) and shifts in ecosystem functioning (see below) associated with the presence of *E. canadensis*.

4.2.2 Macroinvertebrates

Differences in macrophtye community between the lakes were further associated with shifts in the macroinvertebrate communities sampled from the macrophytes (paper II). Community composition of the macrophytes from which the invertebrates were sampled broadly matched that of the wider transects. Samples from the invaded lakes contained some *E. canadensis*, while in the reference lakes, native macrophytes *Myriophyllum spp (M. alterniflorum, M. spicatum* and/or *M. verticilatum)* were among the sampled macrophyte species. Macrophyte biomass was larger for the samples collected in the invaded lakes (5.735+ 1.219) than in the uninvaded reference lakes (2.535 ± 0.422 g dry weight), with this result near significance at the 5% level ($F_{(1,16)} = 4.182$, $p = 0.058$). The macrophyte biomass reflects the variation in macroinvertebrate abundance and richness between invaded and uninvaded lakes (abundance and richness; invaded lakes, 192 ± 36 and 21 ± 1; reference lakes, 137 ± 18 and 16 ± 1, respectively). The results are noteworthy as they reflect the true nature of the sampled transects, with larger macrophyte biomass retaining more macroinvertebrates in the invaded lakes compared to the univaded reference lakes. Nevertheless, when referring to per gram dry weight of macrophytes, reference lakes showed a tendency for larger invertebrate abundance and richness per g dw of macrophyte biomass ($F_{(1,16)} <3.995$, $p >0{,}063$). There was however, a clear shift in macroinvertebrate community composition between invaded and uninvaded lakes. The top six macroinvertebrate species from the SIMPER output explained over 40 % of the dissimilarity between invaded and uninvaded lakes. Many of these were tubebuilding chironomidae such as *Glyptotendipes* sp. (which explained 14.7 % of dissimilarity). It is likely these species were favoured by high rates of retention of particulate organic matter (POM) within the invaded stands (see section 4.3.1 below). POM is a food source for these chironomides, but also act as a important component when building their tubes for habitation (Kullberg 1988; Pinder 1995; McKie & Pearson 2006).

4.3 Invasive species and effects on ecosystem functions

Multiple indicators of ecosystem function, including the accumulation of organic material, leaf litter decomposition and the biomass accrual and metabolism of biofilms differed between invaded and uninvaded lakes in my field studies (papers II-III). Additionally, my laboratory experiment uncovered effects of the relative abundance of two invasive species, *E. canadensis* and *E. nuttallii*, on macrophye productivity and nutrient uptake rates (paper IV) (see also Figure 8).

4.3.1 Particulate organic matter (POM)

There was more POM in the macrophyte samples from the invaded lakes (1.310 ± 0.289 g dw) than from the uninvaded reference lakes (0.603 ± 0.192 g dw) ($F_{(1,16)} = 4.709$, $p = 0.045$), which was related at least in part to the difference in macrophyte biomass from the individual samples as mentioned above (paper II). Denser stands tends to lock in more POM, important for lake functioning (Carpenter & Lodge, 1986; Asaeda *et al.*, 2010) and central contribution as food resource and substrate for detritivores and microbes (Bundschuh & McKie, 2016). Additionally, it is possible that differences in morphology between *Myriophyllum* spp. and *E. canadensis* are important, though this has not been quantified. Myriophyllum spp. has long slender leaves, most likely letting POM easily through. *Elodea canadensis* is denser in its growth-form, likely trapping more organic material.

4.3.2 Decomposition of organic matter

Decomposition rate (per day) of leaf litter was seen to be higher in invaded lakes compared to uninvaded lakes, and more so in the coarse mesh bags compared to the fine (interaction; $F_{(1,160)} = 11.761$, $p < 0.001$). The elevated decomposition rate indicate that decomposition mediated by invertebrate shredders increased more strongly in the invaded lakes than that mediated by microbes (paper II). This could reflect a potential increase in shredders in invaded lakes, but I found no difference in abundances of shredders that inhabit macrophytes. Rather, this result may reflect differences in activity of heterotrophic microbes. Although ergosterol, a measure of fungal biomass, did not differ between lakes ($F_{(1,160)} = 0.807$, $p = 0.371$), decomposition in the fine mesh bags was slightly greater in the invaded lakes invaded lakes (0.006 ± 0.001; uninvaded, 0.005 ± 0.001 day^{-1}). This is important because decomposition in the fine bags, unlike ergosterol, include all microbial mediated decomposition (bacteria and fungi). The decomposition rate might have become more pronounced if the duration of the deployment of the litterbags in the lakes were prolonged.

I also found evidence that activity of heterotrophic microbes was increased in the nutrient diffusion substrate study (paper III, and see below), suggesting that the presence of *E. canadensis* does alter environmental conditions in a way positive for these organisms. Both the generality and ecological significance of the higher decomposition rate in invaded lakes than in uninvaded is definitely something that should be looked more into. High rates might not necessarily be positive for wider ecosystem integrity. There may be a quicker turn around time of leaves and the energy stored therein in invaded lakes. This puts organisms dependent on allocthonous litter at risk of having less energy available during the remaining time of the season.

4.3.3 Nutrient availability

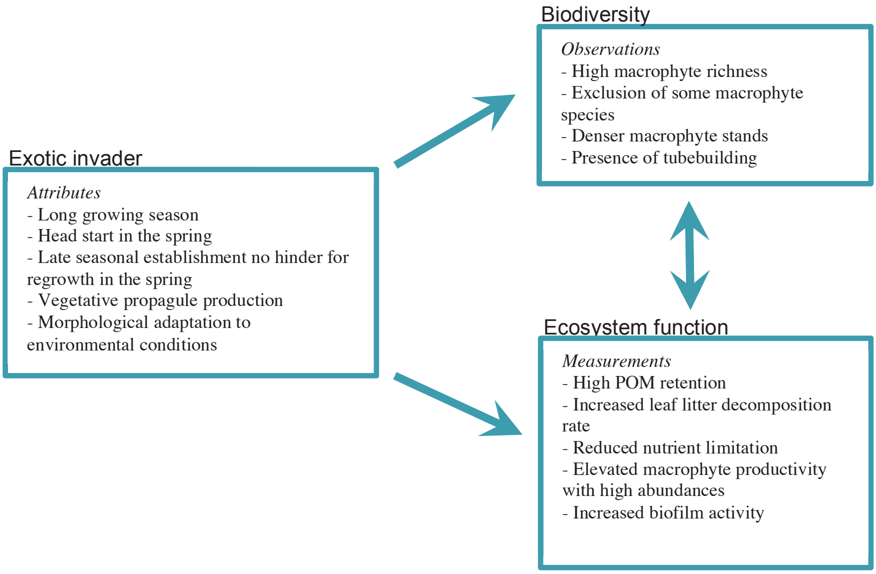
The nutrient diffusing substrate (NDS) experiment (paper III) revealed that the presence of *E. canadensis* is associated with changes in the productivity and metabolism of biofilms on inorganic and organic substrates within macrophyte beds. Growth and activity of autotrophic biofilms on inorganic substrates was particularly affected, with larger chlorophyll-a concentration in invaded compared with uninvaded lakes. That further is reflected in the larger gross primary production (GPP), quantified based on biofilm oxygen dynamics (overall; invaded lakes, 7.53 ± 0.41, and uninvaded lakes 3.73 ± 0.16 $\mu g\ O_2\ cm^{-2}\ hr^{-1}$). Biofilms were overall limited by nitrogen, but nutrient limitation by nitrogen was greater in the uninvaded lakes, affecting both in increased GPP and respiration when nitrogen was added. Finally, the GPP:respiration ratio was greater in the invaded lakes overall, indicating the biofilms became more autotrophic, especially with addition of nitrogen. There were no differences in the overall concentrations of dissolved nitrogen between the lakes, and there was also no evidence of differences in availability of light or grazing pressure.

Accordingly, the results suggest that the macrophyte assemblage and their associated periphyton used up more nitrogen in the uninvaded lakes than in the invaded lakes.

E. canadensis was both productive and an efficient absorber of nutrients when in monoculture in the mesocosm experiment (paper IV). However, nutrient uptake by *E. canadensis* decreased with increasing macrophyte species richness (from one to three; monoculture 0.546 ± 0.055, polyculture 0.377 ± 0.016 µg/mg) and decreasing invasive relative abundance. These results indicate that the two other species present in the mesocosm (*M. spikatum*, *C. demersum* and/or *E. nuttallii*) where more effective in the nutrient uptake than *E. canadensis*. This in turn suggests that the field NDS results might partly reflect disruption of positive macrophyte diversity effects on nutrient uptake when *E. canadensis* is present, but in what way this happens is unclear.

4.3.4 Macrophyte productivity

In the mesocosm experiment (paper IV), I found that net diversity effect and complementarity of macrophyte productivity (measured as relative biomass ratio; difference in biomass between end and start of experiment) both decreased as the number of invasive species increased (both; $F_{(1,50)} > 4.264$, $p < 0.044$). This indicates that larger competition for resources when two invasive species are present reduces rates of productivity. Additionally, drought overall affects macrophytes productivity. Even though the invasive species tended to drive up growth in the non-drought mesocosms. This was cancelled out in the drought-affected mesocosms by their lower level of resistance to drying, and/or slower recovery. Overall, any effects of invasive species presence on recovery from drought were minor and tended to be negative.



Exotic invader

Attributes
- Long growing season
- Head start in the spring
- Late seasonal establishment no hinder for regrowth in the spring
- Vegetative propagule production
- Morphological adaptation to environmental conditions

Biodiversity

Observations
- High macrophyte richness
- Exclusion of some macrophyte species
- Denser macrophyte stands
- Presence of tubebuilding

Ecosystem function

Measurements
- High POM retention
- Increased leaf litter decomposition rate
- Reduced nutrient limitation
- Elevated macrophyte productivity with high abundances
- Increased biofilm activity

Figure 8. Summarising the attributes and impacts of *E. canadensis* on biodiversity and ecosystem functions

5 Concluding remarks and future perspectives

Much of the discussion on invasive species centres on strategies to prevent introduction and spread, as well as control of outbreaks at local scales. The other, and I would claim equally important, is the impact they have on the ecosystem, not only during the first phase of invasion, but also in period after they are well-established. Assessments of impact should focus not only on diversity of similar species, but also other species groups. It should additionally consider associated effects on functioning. Such information is crucial to address the question we need to ask ourselves is why do we need to worry?

I have shown that the invasive macrophyte *Elodea canadensis* is well suited to a life in boreal lakes. It has a competitive growth strategy, and results from my field studies show that it may have a head start after the winter compared to native species. Additionally, important shifts in diversity and community composition of macrophytes and invertebrates associated with macrophyte species rich areas, where the macroinvertebrate community also reflect this. Increasing abundance of invasive species in laboratory settings showed to increase macrophyte community productivity with relations to biomass, but did not stabilize the community after drought. I have also shown elevated leaf litter decomposition, organic matter accumulation and biomass accrual. Additionally, activity of biofilms were all greater in lakes invaded by *E. canadensis* compared to uninvaded lakes. In conclusion, it is clear that *E. canadensis* is affecting multiple aspects of structure and functioning in our lakes.

Before considering wider implications of my results, it is important to consider some limitation. I understand that, the low number of lakes does not provide a lot of comparable datasets. However, I used a robust statistical design to factor out effects associated with lake and transect identity. Nevertheless, some results might have been influenced by the choice of lakes. Best example is litter decomposition, which did not differ from uninvaded levels in one of the invaded lakes at all, suggesting that a different set of lakes might have yielded different results. Furthermore, it is important to mention that I do not know anything about the invasion history of the lakes used in our field study, making it more difficult to distinguish cause and effect when determining the true effect of an invasive species. Nevertheless, I carefully chose the study systems to represent the typical lake favoured by *E. canadensis*, and thus believe the results are relevant for understanding the wider impacts of *E. canadensis* in this type of lakes.

Given its current level of impact, my findings suggest there are reasons to manage *E. canadensis* on purely ecological grounds. However, it is important to bear in mind the potential for some management actions to do more harm than good. For example, mechanical removal of macrophytes can lead to increased fragmentation as a side effect, increasing risk of further spread (Ozimek *et al.*, 1993; Van Donk *et al.,* 1993; Jeppesen *et al.,* 1998). Furthermore, given the limited resources for management, the impact of *E. canadensis* under different environmental conditions needs consideration, as do its effects relative to other invasive species and environmental disturbances. These and other open questions point to the need for more research beyond mine

There are several important open topics that highlight the value of continued study of *E. canadensis* and other invasive macrophytes

i) Quantify impact in the field: spatio-temporal scales

In general, both temporal and spatial scale is important to consider when evaluating the potential impact of an invasive species (Davies *et al.*, 2005; Strayer *et al.,* 2006). For example, strong local impacts might not be so evident at a whole lake or landscape scale. In my research the large scale implications of changed ecosystem functioning (decomposition, nutrient availability ect.) are unclear. Furthermore the time it actually takes to recognize an impact can also vary. This can be tightly linked to propagule pressure and habitat disturbance that might favour the invasive species. It is therefore difficult and uncommon to trace the whole invasion history of a species in a potential lake or stream, and so in most cases any single assessment will represent a snapshot of an invasion stage. These snapshots are however valuable as they quantify impacts in the field. A lot of studies are based on laboratory experiments. They are performed under strict conditions and cannot always relate to field observations. The information gained from field studies will improve and support management decisions. Therefore we should not only focus on the periods of population explosion, but also look into times when the invasive species is not dominating the ecosystem (Strayer *et al.,* 2006). It is further important to consider the seasonal variation in biomass production when deciding when to initiate sampling campaigns. Additionally, information on local scale should be combined with modelling to determine broader landscape impacts.

ii) Continuous potential spread

I found that *E. canadansis* does not seem at all restricted by the strong seasonality characterising of boreal habitats. The invasive macrophyte may rather even have an advantage over native species in being able to establish late in the season. This suggests great potential for further spread into currently uninvaded systems northwards. It is therefore important to minimize the spread, by being aware of its spread pathways, and survival- and establishment potential for the vegetative fragments.

iii) Model species for future invasive submerged macrophytes

Boreal lakes are situated in the north of the northern hemisphere. For several invasive species in central Europe, the environmental conditions are already favourable for spread further north. They have just not managed to get there yet. Potential invading macrophytes are *Azolla filiculoides, Crassula helmsii, Lagarosiphon major, Lemna minuta, Myriophyllum aquaticum* and *Zizania aquatic* amongst others (Hallsten, 2005). The current climate change is also increasing this pressure, where previously hostile environments with cold, long winters may get far more favourable conditions for invasive species (Dukes & Mooney, 1999; Hellmann *et al.*, 2008). There are very few invasive macrophytes that have established in boreal lakes so far (eg. in Sweden, Naturvårdsverket, 2010). It is therefore favourable to use an established invasive species like *E. canadensis* as a model species. *Elodea canadensis* has many of the attributes that are central for an invasive species to establish and spread, and this can be used to quantify impacts that potentially new invasive macrophytes might have.

iv) Effects of multiple stressors

Humans demand on natural habitat, increase pressure on ecosystems. Currently, aquatic ecosystems are impacted by multiple stressors (Vörösmarty *et al.*, 2010). On the one hand these stressors might affect the susceptibility of aquatic ecosystems to invasion, whilst also regulating the strength of impact those invasive species might have (Strayer, 2010; Ricciardi *et al.*, 2013). Invasive species, such as *E. canadensis*, will only be part of a larger "stressor picture". It will be important to establish and quantify effects of multiple stressors on *E. canadensis*, but also with the invasive macrophyte being one of multiple pressure points. We need to get knowledge of which stressors that tend to exaggerate the impact of invasive species. It is also beneficial to recognise when an invasive species help to buffer the effect of a stressor before initiating mitigations against this species.

Raising consciousness

The further invasions by nonindigenous species into boreal lakes seem inevitable. We need to be aware of the species that are "on our doorstep". It will be essential to decrease spread and achieve insight into potential effects on native habitat. Understanding of *E. canadensis'* attributes and impacts can help management and decision makers prepare for new macrophyte species invasions. Raising public consciousness on the presence and impacts of an invasive species like *E. canadensis* is crucial. We need to be aware of the changes that are happening in our environment, and realize that we are a large contributor to the species continuous spread. But most important of all is to underpin the importance of understanding the sensitivity and value of uninvaded habitats, that become ever more rare.

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Popular science summary

It is a nice hot day and you cannot wait to take a dip in the lake. The only drawback is the annoying plants that keep touching when you swim?! They feel slimy and are only in the way! But is this really all that is going on?

Underneath the surface of the water, there is a whole new world that opens up. The aquatic plants known as macrophytes are to lakes what trees are to terrestrial habitats. As such they underpin the biodiversity and activities (ecosystem functions) of other lake organisms. Aquatic macrophytes provide refuges for fish, insect larvae and animal plankton. Macrophytes also absorb nutrients from the water dramatically reducing the chances of harmful algal blooms, which otherwise could transform the lake into a green soup. Aquatic plants are also important for stabilizing the lake-bottom with their roots. Each lake has its own combination of macrophytes, but the balance of these assemblages can be disrupted by the invasion of non-native plants. Such invasive plants can take over and crowd out other native species, affecting biodiversity and the ecosystem functions mediated by the native plants.

The Canadian water weed (*Elodea canadensis*) is such a non-native species in boreal lakes across Scandinavia. It is considered non-native because its actual native area is North America. A botanist in England thought it looked nice and planted it in the pond in the botanical garden where he worked. It was the start of an invasion across Europe! Today, Canadian waterweed continues to be widely used in home aquariums and garden ponds.

The Canadian waterweed has now been in Sweden for over 100 years. Firmly established in the south and northwards along the coast. However, it has still the potential to spread further north into sensitive regions which up to now have been subjected to relatively low rates of invasion. The species is increasingly regarded as "naturalised" in some other regions of Europe suggesting any ongoing impact is very minor. My research focussed on whether it can similarly be regarded as "naturalised" in Sweden, or whether it continues to have major impacts on biodiversity and ecosystem functions. I also investigated the special attributes of the species that contribute to its capacity to spread and its level of impact.

To begin with I discovered that Canadian waterweed is able to establish from plant fragments very late in the autumn. They regrow early in the spring giving it a competitive advantage compared to other native species that barely started regrowing at the time of the inventory (end March). Further, it does best when growing by itself, as the internal competition, facilitates the growth of single plant individuals. The species can hence form dense monocultural stands, shutting out native species. I found that this does not necessarily reduce species richness but does change macrophyte species composition. For example, a well-known native macrophyte group, the watermilfoils (*Myriophyllum* spp) was almost completely absent in our studied lakes invaded by Canadian waterweed. These changes also have potential to affect other aquatic organisms associated with the plants, reflecting changes in the habitat architecture provided by the plant assemblage. Additionally I discovered that the aquatic insect larvae composition was altered by the presence of Canadian waterweed.

Finally, the presence of an invasive species, introducing particular attributes into an ecosystem, has the potential to alter the way the ecosystem processes nutrients and energy. I found that the presence of the species increases leaf litter decomposition and retention of organic matter. Increases in processes such as litter decomposition are not necessarily good. For example, decomposition that occurs too fast might deplete the terrestrial source of energy in the system, much too early in the season and cause drastic effects later on.

I also found that productivity of algal biofilms also increases when Canadian waterweed is present, but this was because nutrient uptake by the macrophyte assemblage as a whole was reduced. Given that macrophyte beds normally take up lots of nutrients this might indicate that overall nutrient absorption capacity is reduced in macrophyte stands including Canadian waterweed. Further I observed through an experiment that the presence of two invasive macrophytes (Canadian waterweed and the closely related Western waterweed (*Elodea nuttallii*)) tended to be associated with negative effects on ecosystem functioning.

My results suggest that Canadian waterweed continues to have important impacts on biodiversity and ecosystem functions in Swedish lakes. This should be considered by managers when developing management strategies for invasive macrophytes, such as Canadian waterweed, Western waterweed, and a probable invader Parrot's feather (*Myriophyllum aquaticum*) to name a few.

Populärvetenskaplig sammanfattning

Det är en fin sommardag och du kan knappt bärga dig till att ta ett dopp i sjön. Visst är det irriterande att få vattenväxter som snurrar sig runt benen på dig när du simmar?! De känns slemmiga och är bara i vägen! Men vad ligger egentligen bakom att det här händer?

Under vattenytan öppnar en helt ny värld upp sig. Vattenväxterna som kallas makrofyter är för sjöar vad träd är för landhabitat. Som sådana stöttar de biodiversiteten och olika aktiviteter (ekosystemfunktioner) för andra organismer i sjön. Akvatiska makrofyter erbjuder skydd för fiskar, insektslarver och djurplankton. Makrofyter absorberar också näringsämnen från vattnet och minskar därmed dramatiskt chanserna för skadliga algblomningar, som annars kan förvandla sjön till en grön soppa. Vattenväxter är också viktiga för att stabilisera sjöbottnen med sina rötter. Varje sjö har sin egen kombination av makrofyter, men balansen i denna sammansättning kan störas av invasionen av främmande arter. Sådana invasiva växter kan ta över och konkurrera ut andra inhemska arter och därmed påverka biodiversiteten och ekosystemfunktionerna som de inhemska arterna medfört.

Vattenpesten (*Elodea canadensis*) är en sådan främmande art i boreala sjöar i Skandinavien. Den är främmande för att den egentligen är inhemsk i Nord-Amerika. En botaniker i England tyckte den var fin och planterade den i en damm i den botaniska trädgården där han jobbade. Det blev starten på en invasion i Europa! I dag fortsätter vattenpest att säljas som akvarieväxt.

Vattenpesten har nu funnits i Sverige i över 100 år. Väl etablerad i de södra delarna och norrut längs kusten. Den har dock fortfarande potential att spridas längre norrut till känsliga regioner som hittills har varit relativt förskonade från invasioner. Arten ses allt oftare som ”naturlig” i vissa andra delar av Europa vilket tyder på att dess pågående påverkan är låg. Min forskning fokuserade på huruvida den kan anses vara ”naturlig” även i Sverige eller om den fortfarande har stor påverkan på biodiversitet och ekosystemfunktioner. Jag undersökte även artens speciella egenskaper som bidrar till dess förmåga att spridas och dess nivå av påverkan.

Till att börja med fann jag att vattenpesten kan etablera sig från växtfragment väldigt sent på hösten. De återväxer tidigt på våren vilket ger en konkurrensfördel jämfört med inhemska arter som knappt börjat återväxten vid tiden för inventeringen (slutet av mars). Vidare så klarar den sig bäst när den växer ibland sina egna, eftersom den interna konkurrensen stimulerar tillväxten hos individuella växter. Arten kan därmed forma täta monokulturer och stänga ute inhemska arter. Jag fann att detta inte nödvändigtvis medför en lägre artrikedom men ändrar sammansättningen av makrofytarter. Till exempel saknades den välkända inhemska makrofytgruppen slingväxter (*Myriophyllum* spp) nästan helt i de sjöar vi studerade som invaderats av vattenpesten. De här förändringarna kan också påverka andra vattenlevande organismer som är förbundna med växterna på grund av de boställen och gömställen de utgör. Jag upptäckte att sammansättningen av olika arter av vattenlevande insektslarver förändrades av förekomsten av vattenpest.

Slutligen har förekomsten av en invasiv art som introducerar vissa egenskaper i ett ekosystem potential att förändra sättet som ekosystemet utnytter näringsämnen och energi. Jag fann att förekomst av arten ökar nedbrytningen av löv och bibehållande av organiskt material. Ökningar i processer som nedbrytning av löv är inte nödvändigtvis av godo. Till exempel kan nedbrytning som sker för fort uttömma den terrestra energikällan i systemet alldeles för tidigt på säsongen och orsaka stora effekter senare på säsongen.

Jag fann också att produktiviteten hos alg-biofilmer ökar då vattenpest finns närvarande, men detta berodde på att näringsupptaget hos makrofyt-sammansättningen minskade som helhet. Då makrofytbäddar normalt sett tar upp stora mängder näring kan detta indikera att det totala upptaget av näring är mindre i makrofytsammansättningar där vattenpest förekommer. Vidare fann jag i ett experiment att förekomst av två invasiva makrofyter (vattenpest och den närbesläktade smal vattenpest (*Elodea nuttallii*)) tenderade att vara förknippade med negativa effekter på ekosystemfunktioner.

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