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Modelling the risks of invasive aquatic species spread in Swedish lakes

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Summary

Species distribution modelling is a valuable tool for identifying areas most at risk of the spread of invasive species. Here we model the environmental factors governing the distributions of two invasive species of concern that are currently found in Sweden at only a limited number of locations: the aquatic macrophyte *Elodea nuttallii* (Nuttall's waterweed / smal vattenpest) and the bivalve *Dreissena polymorpha* (Zebra mussel / vandrarmussla). For *E.nuttallii,* the greatest risk factors are connectivity with other water bodies (facilitating dispersion), human population density and length of growing season. This implies that it is principally well-connected lakes in populated areas of southern Sweden that are most at risk of further spread (although other areas of concern are identified). For *D.polymorpha*, water alkalinity and the proportion of agricultural land (a source of nutrient pollution) are the most important factors, and the models identify lakes Vänern and Vättern, waters in parts of Östergötland, Jämtland and Gotland as key areas of concern for further spread.

1 *Elodea nuttallii* - Introduction

Human activities have resulted in the spread of many species to new locations where they may have undesirable effects, whether ecological, social, or economic. Climate change has further enabled invasive species to follow climatic niches to new locations, and aquatic macrophytes are among the many species that have already responded to recent climate change by expanding their ranges in Europe (Alahuhta *et al.*, 2011). As a result, it is projected that there is a high risk of colonisation of new areas by invasive macrophytes (Gillard *et al.*, 2017). This poses a risk to the biodiversity and ecosystem functioning of these areas, as well as to the services provided by these ecosystems, such as bathing, boating, and fishing. To minimise the spread of invasive species and the subsequent negative impacts, it is important to be able to predict the distribution of invasive aquatic plants of concern, identifying areas that are most at risk of being colonised so that monitoring and removal efforts can be appropriately targeted.

Figure 1: Elodea nuttallii. By Christian Fischer, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=15559437

We focus in this part of the report on *Elodea nuttallii*, an invasive aquatic macrophyte with currently only limited spread in Sweden (Fig. 1). *E. nuttallii* (and the closely related *Elodea canadensis*) are native to the temperate areas of North America but were introduced to Europe for use as an ornamental plant in ponds and aquariums. *E. nuttallii* was first recorded in Europe in Belgium in 1939, followed by observations in the Netherlands and Germany in the 1940s and 1950s. It was not formally recorded in Sweden until 1991 (Anderberg 1992), although it was probably present earlier, with some observations from the public recorded in Artdatabanken during the previous decade. *E.nuttallii* is listed as an invasive alien species of EU concern under Regulation 1143/2014 of the European Parliament on the prevention and management of the introduction and spread of invasive alien species (CIR 2017). The *Elodea* species are problematic as they can form dense stands that displace other macrophytes, hinder boat traffic, block the inflows of hydroelectric plants and make water bodies unsuitable for recreational activities such as swimming. These stands also decay in autumn and winter, resulting in a rapid release of nutrients that can negatively impact water quality. *E.canadensis* is longer established in Sweden and is currently more widespread than *E.nuttallii* but given the similar environmental preferences of the two species, it is assumed that *E.nuttallii* has the capacity to establish in many areas where it has not yet been found (i.e., at least those areas where *E.canadensis* has been found are potentially hospitable for *E.nuttallii*).

Objectives of the study

- To model the current distribution of an invasive macrophyte species, *Elodea nuttallii*, in the lakes of Sweden.
- To disentangle the relative influence of different categories of environmental factors acting at local and catchment scale on *E.nuttallii* distribution.
- To predict the current invasion risk in areas where *E.nuttallii* has not yet been recorded.

1.1 *E.nuttallii*'s environmental niche

Light

E.nuttallii is tolerant of low light conditions (Mielecki & Pieczynska, 2005), a common trait of *Elodea* species (Abernethy *et al.*, 1996). However, *E.nuttallii* is able to cope with low-light conditions better than *E.canadensis* (Barrat-Segretain, 2004).

Depth and flow

Both Elodea species, *E. nuttallii* and *E. canadensis*, are commonly found in lakes and slow flowing rivers in shallow water, typically at a depth of less than 3 meters (Simpson, 1990). *E.nuttallii* may survive in deeper water than *E. canadensis* (Anderberg 2005); however, it grows best in shallower waters.

Nutrients and water chemistry

E.nuttallii is mainly found in eutrophic, meso- or oligotrophic waters with a degree of organic pollution (Best *et al.*, 1996). It thrives best in waters with a pH ranging from 7 to 9 and has a preference for higher concentrations of calcium (Jones *et al.*, 1993). Furthermore, *E.nuttallii* is able to survive in waters with a salinity up to 14 ppm (Josefsson 2011). Nitrogen fertilisation also seems to be beneficial for its growth (Dendène *et al.*, 1993).

Temperature

Growth of *E. nuttallii*, which generally occurs at temperatures above 10 °C (Kunii, 1984) has been observed to occur at a significantly slower rate at a temperature as low as 4 °C (Kunii, 1981). In many lakes, winter temperatures are unlikely to fall below 4 °C, meaning that there may be very slow growth rather than winter dormancy in these conditions.

1.2 Reproduction and lifecycle

E.nuttallii is dioecious (i.e., plants have either male or female reproductive organs), and in Europe only female plants are thought to be present. Consequently, reproduction is entirely vegetative, although this is by no means a limitation on spread, and even small plant fragments can form roots and start growing. Indeed, vegetative reproduction facilitates effective dispersal, with plant fragments freely transported downstream. Water birds can act as a transport vector between unconnected water bodies (Sand-Jensen *et al.*, 2000), but human activity is more important in this regard, and the movement of small recreational boats between lakes seems to be an important dispersal factor. A key limitation for both *E.canadensis* and *E.nuttallii* is that their propagules cannot survive drying (Sand-Jensen 2000).

E.nuttallii has often been seen to have a competitive advantage over *E. canadensis,* especially in nutrient rich waters. This may be due to *E.nuttallii*'s high growth rate in eutrophic conditions, its higher colonisation ability than *E.canadensis*, and faster regeneration in the spring, all factors which help it outcompete *E.canadensis* where both species are present (Barrat-Segretain, 2004).

1.3 Impact of *E.nuttallii*

1.3.1 Ecological impacts

Elodea (both *nuttallii* and *canadensis*) can grow rapidly and form dense stands that can monopolise the supply of light, thereby displacing other aquatic plants. This displacement of other plants due to shading and competition for nutrients from *Elodea* threatens several endangered aquatic plant species, such as *Najas flexilis* (sjönajas) in Norway (Brandrud & Mjelde, 1999) and *Najas tenuissima* (spädnajas) in Finland. This negative effect is most pronounced in more nutrient rich localities where the degree and duration of mass occurrences is greatest.

Such a drastic change in the plant community in a water body obviously has impacts on a range of other species that depend on plants for food or habitat, which are often negative, but in some cases may be positive. During the growing season *Elodea* takes up nutrients to such an extent that other macrophytes and phytoplankton can suffer from lack of P and N (van Donk *et al.*, 1993). *E.nuttallii* is flexible in its use of different nutrient sources from both the water and the sediment (Angelstein & Schubert, 2008). However, large masses of *Elodea* leads to large amounts of decomposing matter, which can create hyper-eutrophic and anoxic conditions that are inhospitable for most invertebrates and fish (Nino *et al.*, 2005). This increased availability of nutrients can in turn cause algal blooms (Larson & Willén, 2007). *Elodea* spread has been shown to have negative consequences for native macrophytes in Scandinavia and elsewhere, resulting in decreased biodiversity (Mjelde *et al.*, 2012). Crayfish have also been negatively affected, due to habitat loss, although *Elodea* can provide refuge for juveniles (Hessen *et al.*, 2004). Interestingly, North American crayfish feed extensively on *Elodea*, but the for Scandinavia indigenous *Astacus astacus* generally does not (Lodge, 1991). Some species of waterbirds which feed on *Elodea* can benefit from the increased availability of food (Sand-Jensen *et al.*, 2000).

1.3.2 Economic / social impacts

Dense mats of *E.nuttallii* form in the spring and summer and can become free floating as the plant's roots decay in the autumn. These can severely hinder a range of water uses. Dense stands make water bodies unsuitable for a range of recreation activities such as bathing, fishing and boating, while the free-floating mats can block the inflows of hydroelectric power plants and other industrial users of lake and river water, with economic damage as a consequence (Clayton & Edwards, 2006). In hard water areas calcium can encrust *Elodea* plants and cause damage to boat hulls, a phenomenon reported in Lake Mälaren (Josefsson & Andersson, 2001). *Elodea* growth can also reduce or block the flow in drainage channels with an associated increase in flooding risks (Larson, 2003). Given these substantial undesirable effects of *Elodea* growth, efforts to eradicate or control it may be required, which entail considerable costs. These costs are not only economic, as available methods of control such as water level drawdown, sediment dredging, introducing fish to consume *Elodea*, and the application of herbicides also have ecological costs of their own (Bowmer *et al.*, 1995).

2 Methods

Grid cells are often used for large spatial scale modelling of terrestrial species, but for freshwater species, grid cells are less relevant as some cells may not contain any aquatic habitat. Grid cells also cannot account for the spatial structure of freshwater networks and their connectivity, which is often vital for the spread of invasive species. Despite these limitations, grid cells have been used to model the distribution of macrophytes at large scale (e.g., Alahuhta et al. 2011, Gillard et al. 2017). However, here we use an alternative method of explicitly modelling water bodies using polygons (usually with one polygon per lake but with several for larger lakes) and the connectivity between them in order to more accurately reflect the distribution of habitats that are actually available to the modelled species.

2.1 Data sources

1) *Study area: lakes of Sweden*
    - 37779 lakes (GIS layer from SMHI, digitized from a 1:50000 scale map), with each covered by a polygon (some large lakes are divided into multiple polygons).
    - Each lake has associated with a hydrological catchment based on connectivity (GIS layer provided by SMHI, digitized from a 1:50000 scale map).

2) *Elodea nuttallii data*
    - Occurrence data collected from two different sources:
        - National macrophytes inventory program between 2007 and 2021, providing both presences and absences (importantly, these are true absences as a standardized inventory protocol was followed). Data obtained from the national data host at SLU which provide data via Miljödata MVM (https://miljodata.slu.se/mvm/), a website of environmental monitoring data maintained by the Swedish University of Agricultural Sciences (SLU).
        - Artdatabanken, the Swedish Species Observation System: presence only records for the 2000-2021 period (https://www.artportalen.se/).
    - The geographical coordinates of occurrence records were matched with the lakes polygon layer to provide environmental variables measured at the lake scale.
    - *E.nuttallii* was considered to be present in a lake when the number of occurrence records were ≥ 1. Some lakes have been sampled several times and larger lakes have also been sampled along multiple transects over the lakes' shorelines. There are in some cases a large number of observations from the public in Artdatabanken for the same water body (especially several that are popular for recreational use near main population centres).
    - There are a total of 97 lake polygons where *E.nuttallii* has been detected and 286 lake polygons where *E.nuttallii* has been searched for but not detected. Note that there are numerous observations from Artdatabanken along the Baltic coastline, especially in the Piteå/Luleå area, which are much further north than almost all inland observations (Fig. 2).

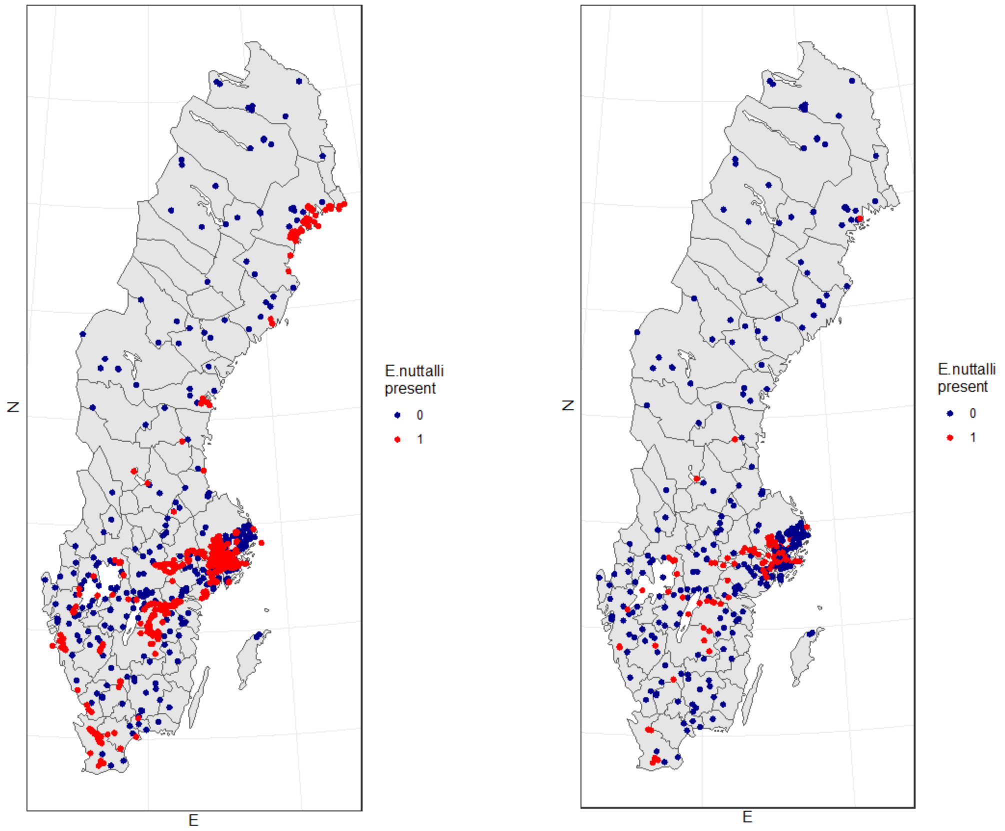

Figure 2 All observations and confirmed absences of E.nuttallii (left), only those observations and confirmed absences that are matched to a lake (right)

3) Environmental data/ explanatory variables

An initial selection of environmental factors was based on a literature review on the ecological preferences of *Elodea* and other freshwater macrophytes (e.g., Bornette & Puijalon 2011, Buchan & Paddilla 2000, Son et al. 2017). However, some variables were selected in a first step but then removed either because data were not available, or with insufficient variability at the scale of Sweden.

Strong correlations between predictor variables causes unreliable estimates in modelling using regression methods, and a check was therefore made for multicollinearity between variables using the Variance Inflation Factor (VIF) function of the R package 'usdm' (Naimi et al., 2014). As expected, several variables showed unacceptably high values (VIF > 10), and a stepwise procedure of removing the variable with the highest VIF until all remaining variables have a VIF <10 was used to produce a final list of explanatory variables. The following categories and variables were included.

Physical features of lakes:

- Mean depth of the lake: estimated using a statistical regression based on 6618 lakes (Sobek et al. 2011). This is included as *E.nuttallii* growth is light limited and cannot occur at greater depths than 4-5 meters.

- Cumulative length of shorelines: total length of shorelines for each water surface, including islands within lakes (as these are suitable habitats for *E.nuttallii* which prefers shallow waters).

Connectivity:

- Number of lakes upstream: measured using the stream network and connectivity between lakes (SMHI).
- Distance to sea: as *E.nuttallii* can be found in brackish waters, and numerous coastal observations have been made along the Baltic coast, the sea is a potential source of propagules.

Water chemistry/quality (water chemistry data were not available for all the lakes so to achieve greater coverage the following proxies were used):

- Agricultural area. The proportion of agricultural areas was used as a proxy for nutrient concentrations within each catchment. Nutrient concentrations increase in areas with high agricultural usage and may benefit the growth of *E.nuttallii*. The proportion of agricultural areas was derived from the CORINE (European Union, 2018) land cover at a resolution of 250 x 250 m.
- Peat. The proportion of peats within catchment was used as a proxy for water colour (more peats result in browner waters).
- Alkalinity. Spatial interpolation (kriging) of measured alkalinity for 5709 lakes. Provided from national monitoring program Omdrevssjöar (SLU) via Miljödata MVM.
- pH. Spatial interpolation (kriging) of measured pH for 5709 lakes. Provided by Omdrevssjöar database, Institutionen för Vatten och Miljö (SLU).
- Nitrogen deposition. Data from the European Monitoring and Evaluation Programme deposition model (Simpson et al., 2012, 2020) on a 50 x 50 km grid. Values of ammonia (mg N/m^2) and nitrate (mg N/m^2) were interpolated for each lake.

Habitat availability:

- Open water. The proportion of open waters within each catchment, taken from CORINE land cover at a resolution of 250 x 250 m and used as a proxy for habitat availability for *E.nuttallii*.
- Wetland. The proportion of wetlands within each catchment taken from CORINE land cover at a resolution of 250 x 250 m and used as a further proxy for habitat availability for *E.nuttallii*.

Human impacts:

- Built-up area. The proportion of built-up areas within each catchment takenfrom CORINE land cover at a resolution of 250 x 250 m. *E.nuttallii* is more abundant in areas close to human activities due to dispersal by boats, fishing etc.

- Human population density. Population density data from SCB (Statistiska centralbyråns, Statistics Sweden) at 1 x 1 km resolution.
- Holiday homes. The density of holiday homes, data from SCB (Statistiska centralbyråns, Statistics Sweden) at municipality level.

Climate:

- Number of growing degree days above 5°C. The number of days above 5°C for mean daily temperature, which according to the literature is the threshold for active growth of *E.nuttallii*.
- Number of frozen days below zero. The number of days with a mean daily temperature lower than 0°C. This is included to reflect the possibility that *E.nuttallii* fails to survive in lakes that are frozen for lengthy periods.

Plots of the rasters based on the above variables used in the modelling can be found in Appendix 1.

2.2 Modelling methods

Species distribution modelling (SDM) is based on three key steps. Firstly, the environmental characteristics of those sites where the target species is found are examined. Second, a statistical model is produced to define the species' requirements and preferences in terms of environmental conditions. Finally, the model is used to identify locations that are suitable habitats for the species, facilitating the identification of areas of highest risk for spread (Peterson & Vieglais, 2001).

The selection of a particular modelling algorithm in a correlative SDM can have strong effects on the model outputs, with some methods performing much better than others in specific cases. This variability means that there is no "best" method in a general sense (Segurado & Araújo, 2004). As a result, the approach of combining different modelling methods to produce an ensemble prediction was developed (Araújo & New, 2007), which mitigates the risk of choosing a single method which may perform poorly in a specific set of circumstances. We here use the best-established implementation of this approach, the R package Biomod2 (Thuiller, 2003). This applies a range of modelling techniques (generalised linear models, GLM (McCullagh & Nelder, 1989), generalised additive models, GAM (Hastie & Tibshirani, 1990), multivariate adaptive regression splines, MARS (Friedman, 1991), classification tree analysis CTA (Breiman & Ihaka, 1984), mixture discriminant analysis MDA (Hastie *et al.*, 1994), artificial neural networks ANN (Ripley, 2007), generalised boosted models GBM (Ridgeway, 1999), and random forests (Breiman, 2001) before combining their predictions (using both a minimum predictive accuracy threshold for inclusion and a weighting based on their predictive accuracy on test data) to produce an ensemble model.

The evaluation of individual model performance was based on metrics derived from a confusion matrix-area under curve (AUC) of receiver operating characteristics (Hanley & McNeil, 1982), and true skill statistics (TSS) (Allouche *et al.*, 2006). These are indicators of discrimination capacity, i.e., a quantification of how well the model distinguishes presences from absences. The models were trained on a randomly selected 80% of the data and tested on the other 20% of the original dataset.

The following interpretation of AUC-values is a useful guideline when reading modelling results such as these (Swets, 1988): AUC>0.9: excellent agreement between observed and predicted distribution; 0.8<AUC<0.9: good model accuracy; 0.7<AUC<0.8: fair; 0.6<AUC<0.7: poor; AUC<0.6: fail.

3 Results

3.1 Results of ensemble modelling

3.1.1 Predictive performance of the models

For the models created, the mean TSS is 0.63, and the mean AUC is of 0.85. The models can therefore be classified as having good accuracy, although they do not perfectly predict the distribution of *E.nuttallii*. As expected, the scores are somewhat variable, depending on the modelling method used (Fig. 3). Random Forest and GBM perform best, while CTA and GAM have the weakest performance. Note that when included in the ensemble model, contributions are performance weighted.

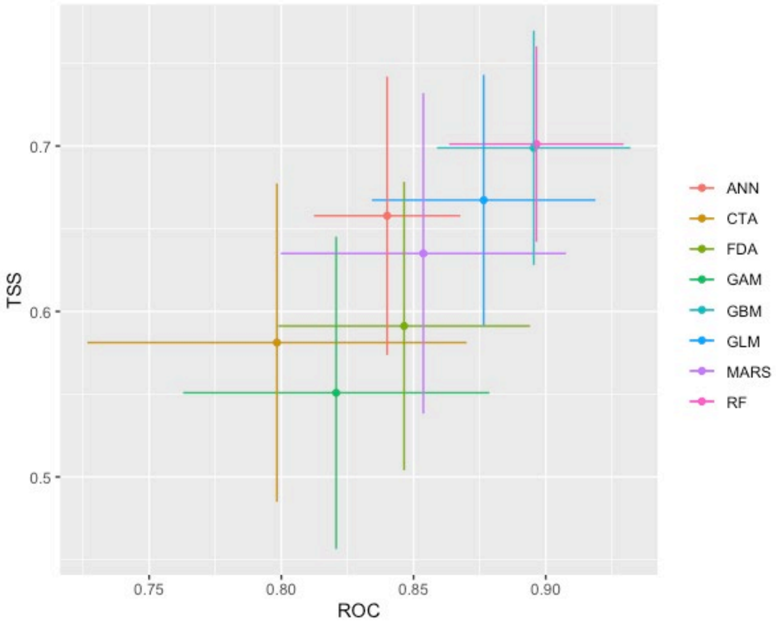

Figure 3: TSS and ROC values for each statistical method used (30 replicates) for E. nuttallii.

3.1.2 Variable importance

The variables contributing the most to the probability of modelled occurrence of *E.nuttallii* in Swedish lakes (according to the mean of importance across algorithms) are the number of lakes upstream (22 %), population density (19%), and the length of plant growth season (18 %). Then come lake shore length (7%), lake depth (7%), alkalinity (6%), and pH (5%). The remaining variables all explain less than 5% - ammonium levels, proportion of built area, distance to the sea, density of holiday homes, proportion of agricultural land, proportion of mud, proportion of wetlands, proportion of open water and proportion of peat. (Fig. 4).

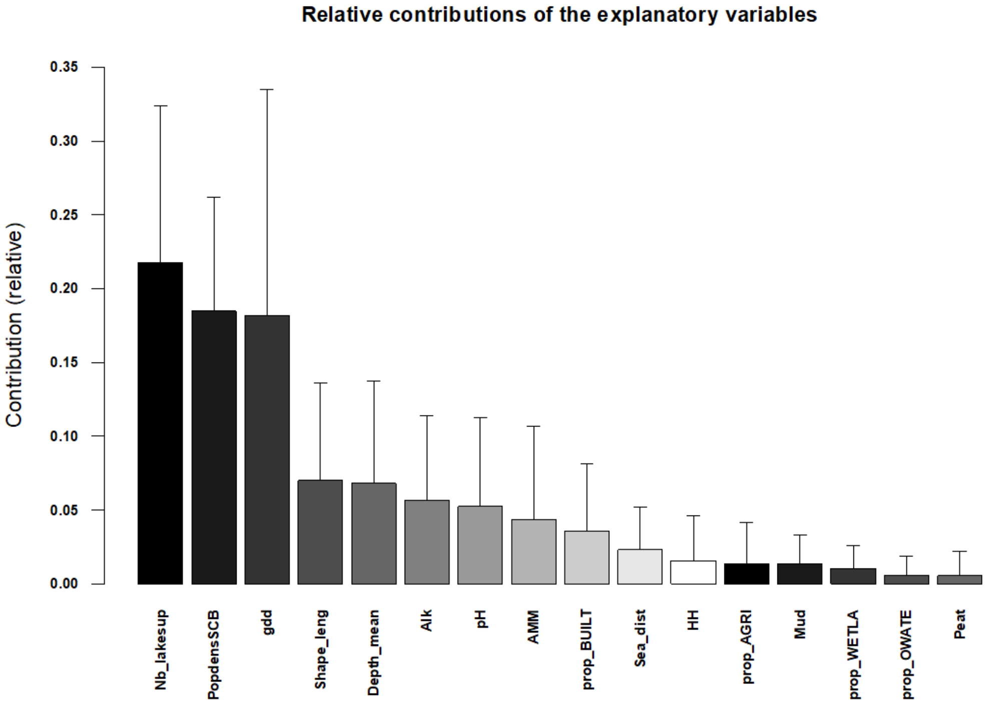

Figure 4: Relative contributions of explanatory variables for E. nuttallii. Nb_lakesup - the number of lakes upstream, PopdensSCB - population density, Gdd - length of plant growth season. Shape_leng - lake shore length, Depth_mean - lake depth, Alk -alkalinity, pH. AMM – ammonium deposition, prop_BUILT proportion of built area, Sea_dist - distance to the sea, HH- density of holiday homes, prop_AGRI - proportion of agricultural land, Mud- proportion of mud, prop_WETLA - proportion of wetlands, prop_OWATE - proportion of open water, Peat- proportion of peat.

The response curves for the explanatory variables, shown in Fig. 5, largely reflect the importance shown in Fig. 4. Unexpectedly, ammonia levels show a flat or slightly negative relationship with *E.Nuttallii* occurrence. A possible explanation is that while nutrients such as nitrogen increase growth, the uptake of nutrients (and specifically ammonium) by rapidly expanding patches of *E.nuttallii* has been shown to result in declining levels in water samples (Crane *et al.*, 2020, 2022).

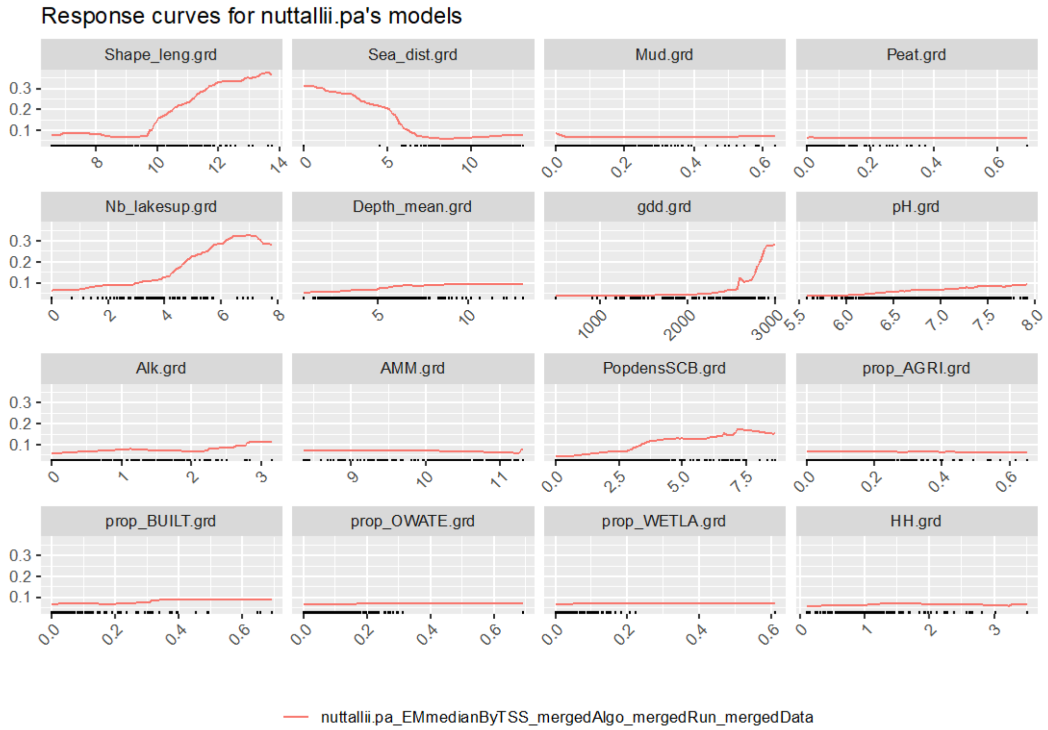

Figure 5: Modelled response curves for the environmental variables used in the ensemble model for E. nuttallii.

3.1.3 Projections based on environmental data

The modelled projection of probability of occurrence is shown in Fig. 6. The highest values are found in the vicinity of population centres in mid and southern areas of Sweden, for example Stockholm and Lake Mälaren, Gothenburg and Malmö (as well as other large highly connected lakes like Vänern and Vättern. Some less populated areas of southern Sweden are also notably high risk, such as areas near the south-east coast (north of Kalmar), while the island of Gotland is another area of concern. Other areas further north are also identified as moderate probability, particularly Jämtland and some areas of Norrland near major rivers flowing from the mountains to the Baltic.

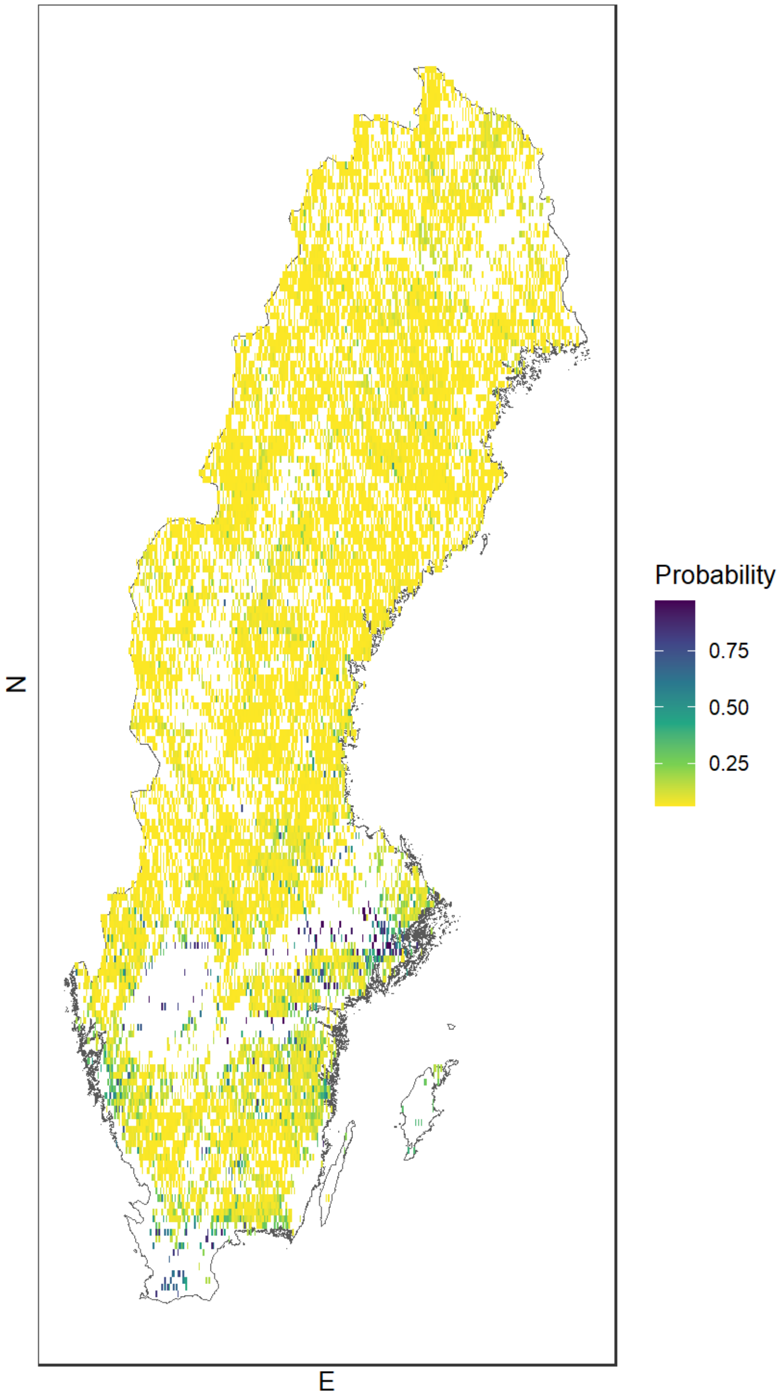

Figure 6: Modelled probability of E.nuttallii in Swedish lakes.

4 *E. nuttallii* - Discussion

The current distribution of *E.nuttallii* in Swedish lakes is mostly limited to well-connected lakes in the southern third of the country (Fig. 2), where human activity is high and growth periods are longer. Our modelling suggests that, indeed, level of interconnectivity with other lakes, human population density and growing season length are the three most important environmental variables for a high probability of *E.nuttallii* presence. This results in a large number of lakes in the southern parts of Sweden that are potential habitats for *E.nuttallii* (Fig. 6), but also some potential for establishment further north. Temperature/growing season is often a limiting factor for invasive aquatic species, and the limited spread in the north of Sweden of *E.canadensis*, despite its presence in the country for around 150 years, suggests that temperature may also be an obstacle for the closely related *E.nuttallii*. However, there are several reports of *E.nuttallii* along the coastline of the Gulf of Bothnia as far north as the Piteå/ Luleå area (Fig. 2) which suggests both that at least air temperatures are not strongly limiting, and that there is a risk of spread inland along waterways from the sea. The modelled variable with the greatest influence on the presence of *E.nuttallii* is the number of upstream lakes, which reflects the fact that the species reproduces by vegetative dispersal of fragments, facilitated by human activities such as boating and fishing, and by animal dispersal. Colonisation from the Baltic coast would need to occur passively from downstream to upstream, which makes natural dispersion more difficult and likely makes human mediated transport a key risk factor. The length of the shorelines and average depth of lakes also increases the probability of occurrence, suggesting that *E.nuttallii* prefers to settle in large lakes with abundant shallow shoreline habitat. The species also shows a preference in terms of water chemistry, with high alkalinity and high pH associated with a higher probability of occurrence.

To conclude, the lakes in Sweden currently most vulnerable to invasion by *E.nuttallii* are relatively large lakes located in the south of the country where growing seasons are relatively longer, in areas with high human population density, and which are downstream of many other lakes. In addition, there is a risk of (particularly human facilitated) spread to inland water bodies from the coast in more northern areas such as Luleå/Piteå and the Sundsvall area.

5 *Dreissena polymorpha* - Introduction

The invasive bivalve *Dreissena polymorpha* (Pallas, 1771), also known as the zebra mussel, is a freshwater filter-feeding mollusc, native to the Ponto-Caspian region lakes in South Russia (Naddafi et al., 2011). The worldwide dispersal of *D. polymorpha* increased significantly during early 19th century. It spread from native populations in the Caspian and Black Seas and it was first recorded in Europe in Rotterdam 1826, Hamburg 1830 and Copenhagen 1840 (Aldridge et al., 2004). The first records of the zebra mussels in Sweden were those found in lake Mälaren in the 1920s (Arwidsson 1926). In the 1970 and 1980s, in the north-eastern basins of Lake Mälaren, the introduction of zebra mussels has likely decreased the negative effects of eutrophication and contributed to the improvement in water quality (Hallstan et al., 2010). It is considered one of the most invasive aquatic species in the world, known mainly for the economic and environmental issues connected to the Great Lakes in the USA, which strongly impacted ecosystem structure and function (Hallstan et al., 2010; Naddafi et al., 2011). *D. polymorpha* global expansion is associated mainly with human activities by "hitchhiking" in ballast waters and on the hulls of commercial cargoes via oceanic shipping/inland waters navigation. Leisure activities also play a role, as through fishing and boating it has also spread to isolated lakes and rivers. *D. polymorpha* is known for its biofouling abilities, creating a wide range of environmental and economic impacts (Hosler, 2011). The present core *D. polymorpha* population in Sweden resides in an area situated around Lake Mälaren (Hallstan et al., 2010) and predicting the areas that meet the environmental conditions required by *D. polymorpha* can be used to estimate areas where *D. polymorpha* could potentially expand in Sweden.

Objectives of the study

- To model the current distribution of an invasive bivalve *Dreissena polymorpha*, in the lakes of Sweden.
- To disentangle the relative influence of different categories of environmental factors acting at local and catchment scale on *D. polymorpha* distribution.
- To predict the current invasion risk in areas where *D. polymorpha* has not yet been recorded.

5.1 Dreissena polymorpha’s environmental niche

Successful colonisation of aquatic invasive species is limited to environments that have suitable conditions for reproduction, growth, and survival. Knowledge about *D. polymorpha*’s physiological requirements is necessary to understand why colonisation of some waters is successful and in others not (Pollux et al., 2022). This knowledge is necessary for developing models aimed to predict potential spreading of the species.

5.1.1 Habitat

The typical habitats colonised by *D. polymorpha* are estuaries, rivers, and lakes, particularly where there are firm surfaces suitable for attachment under water (both natural and man-made) like rocks, submerged wood, boat hulls, buoys, docks, and water intake pipes. *D. polymorpha* is usually found in still or slow-moving freshwaters (as adults they have difficulty staying attached when water velocities exceed 2 m/s). The densest population is usually found between 2-11 m in depth (Werner et al., 2005).

5.1.2 Temperature

For successful reproduction of *D. polymorpha* the minimal temperature should be around 12-15 °C (Karatayev et al., 2007) and for the successful development of *D. polymorpha* eggs temperature should be between 12 to 24°C (Sprung, 1987). The lower temperature limit that *D. polymorpha* can withstand is around 0°C and the upper temperature limit is around 33°C (Karatayev et al., 2007).

5.1.3 Calcium

For successful development of *D. polymorpha* eggs, calcium concentration must exceed 12 to 15 mg l^{-1} (Sprung, 1987; Hincks & Mackie, 1997). Additionally, *D. polymorpha* needs approximately 25 mg l^{-1} concentration of calcium to grow their shells but it can be found at times in lower concentrations (< 20 mg l^{-1}) (Whittier et al., 2008).

5.1.4 pH and alkalinity

For successful development of zebra mussel eggs and the veliger larva, the pH should be between 7.4 and 9.4, with an optimum pH at 8.5 (Bowman & Bailey, 1998; Hincks & Mackie, 1997). Total alkalinity should be higher than 0.6 meq/l (https://artfakta.se/artbestamning/taxon/106634).

5.2 Reproduction and lifecycle

D. polymorpha is a dioecious bivalve (have separate sexes, usually with a ratio 1:1) (Mackie, 1991). Females expel the eggs and fertilization takes place externally by the males (Mackie, 1991). Females are extremely prolific, releasing up to 90,000 eggs ind−1 y−1 (Bighiu et al., 2019). Fertilized eggs hatch into trocophores, developing within a day into a free-swimming planktonic veliger for up to a month. The veliger larvae can disperse within lakes or with currents to downstream waters. On global and local scales, human activities have also played an important role for the dispersal of the zebra mussels (Hallstan et al., 2010). The veliger larvae begin the juvenile stage by settling to the bottom on suitable substratum, attaching themselves with an organ consisting of many threads, called byssus. Once attached, the life span of *D. polymorpha* is variable and it can range between 3 to 9 years (McMahon & Bogan, 2001). Adult mussels can voluntarily detach and move around the substrate to find alternative locations (Marsden, 2011).

5.3 Impact of *D. polymorpha*

5.3.1 Ecological impacts

Dreissena polymorpha is one of the most aggressive freshwater invaders in the world, mainly known for the socio-economic impact caused in the US Great Lakes. Besides being a particularly persistent invasive species, it is also a very effective ecosystem engineer, altering the invaded environments and outcompeting native species for food and space (Karatayev et al., 2002). *D. polymorpha* is a filter-feeding bivalve, capable of filtering large volumes of water while feeding mainly on algae, reducing plankton supply and increasing water clarity (Lindim, 2015; Mei et al., 2016). The increase in water clarity allows light to penetrate further in the water column and potentially promote an increase of benthic algae (Mei et al., 2016). In the invaded environments, *D. polymorpha* affects also trophic interactions and food availability for both pelagic and other native benthic species, and affects the rates of other ecosystem processes like mineralization of nutrients, oxygen availability and sedimentation rates (Karatayev et al., 2002; Karatayev et al., 1997).

5.3.2 Economic / social impacts

As well as threatening the diversity and abundance of native species and the ecological stability of invaded aquatic environments, *D. polymorpha* threatens water-dependent commercial, agricultural, aquacultural, and recreational activities. It is known for its biofouling abilities (accumulation of adult bivalves on hard surfaces) through colonisation of power plants, water systems, and industrial water intakes in the Great Lakes region, costing million annually in damages (Warziniack et al., 2021). Recreation-based industries and activities have also been impacted by *D. polymorpha*. Docks, buoys, boats, boat motors, beaches have all been heavily colonised causing unsuitable conditions for fishing, boating and bathing (Hosler, 2011).

6 Methods

6.1 Data sources

1) *Study area: lakes of Sweden:*
   The study area was as described in detail in section 2.1

2) *Dreissena polymorpha data*

- Occurrence data collected from different sources:
  - Swedish environmental monitoring database (https://miljodata.slu.se/MVM): both presence and absence (true absence as a standardized inventory protocol was followed)
  - Public database: Artdatabanken, the Swedish Species Observation System
- The geographical coordinates of occurrence records were overlapped on the lakes layer to ensure correspondence with environmental variables measured at the lake scale.
- *D. polymorpha* was considered to be present in a lake when the number of occurrence records ≥ 1. Some lakes have been sampled several times and larger lakes have also been sampled along several transects spread over the lake's shorelines. There are in some cases a large

number of observations from the public in Artdatabanken for the same water body (especially several that are popular for recreational use near population centres).

- A total of 246 locations were identified where *D. polymorpha* has been detected (Fig. 7).

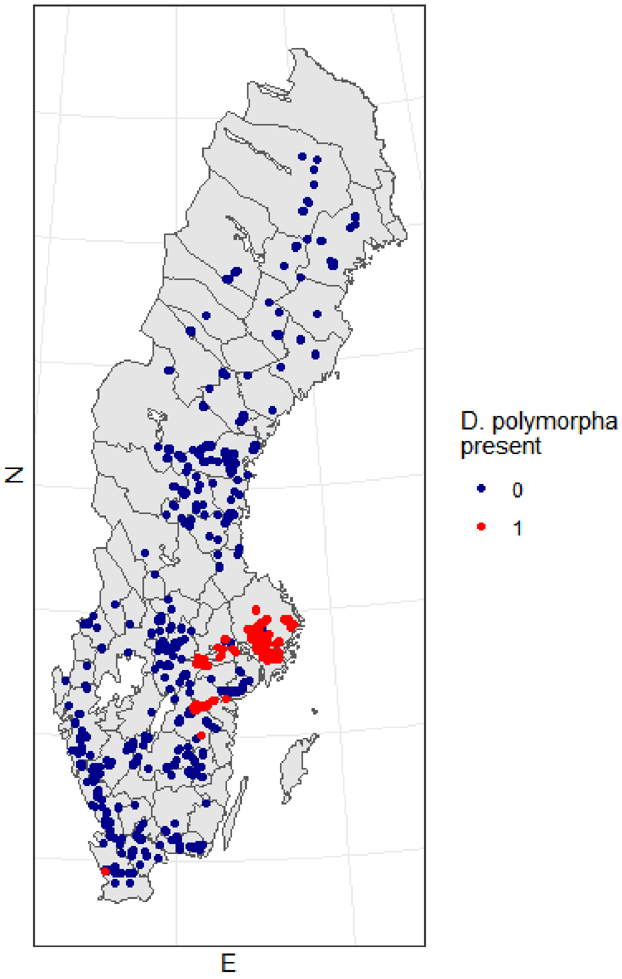

Figure 7: Dreissena polymorpha presences (red colour) and absences (blue colour) in Swedish lakes based on reports from Artdatabanken and monitoring data from Miljödata MVM.

3) *Environmental data/ explanatory variables*
The environmental data were described in detail in section 2.1. Different modelling based on only lakes with measured chemistry is presented in Appendix 2.

6.2 Modelling methods

The modelling methods are described in detail in section 2.2

7 Results

7.1 Results of ensemble modelling

7.1.1 Predictive performance of the models

For the models created, the mean TSS is 0.60, and the mean AUC is of 0.80. The models can therefore be classified as of acceptable accuracy. The scores are somewhat variable, depending on the modelling method used (Fig. 8). The GAM had to be excluded from the modelling options as it kept failing during the modelling run. GBM has the strongest performance, while GLM and CTA have the weakest. Besides GLM and CTA, all modelling methods are adequate to be included in the ensemble models.

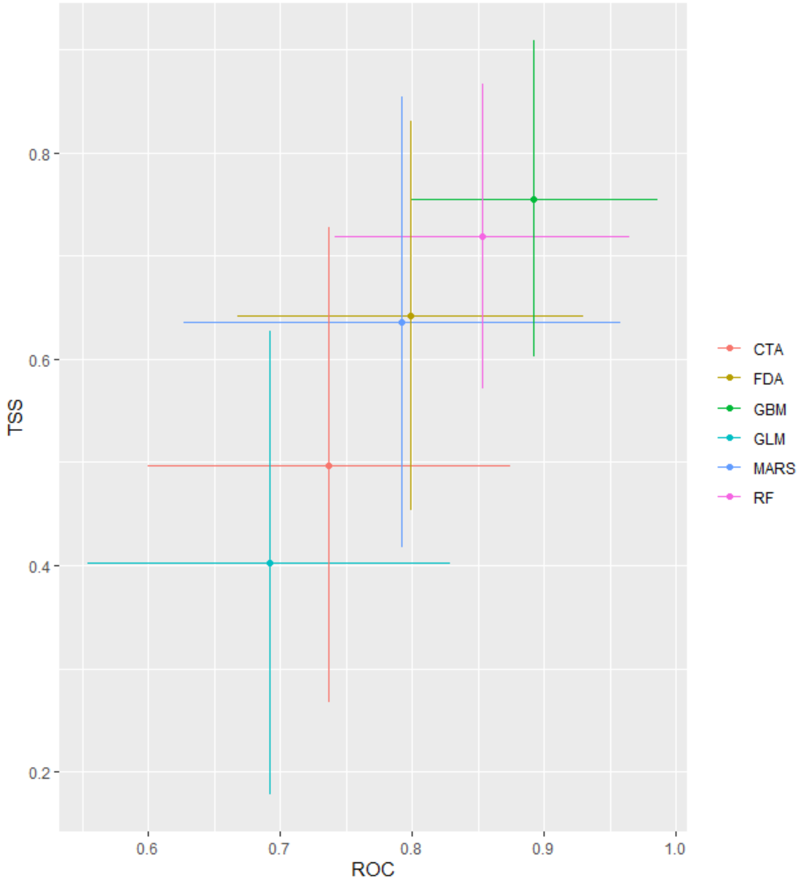

Figure 8 : TSS and ROC values for each statistical method used (30 replicates) for D. polymorpha.

7.1.2 Variable importance

In model calibration, only non-collinear predictors were retained, resulting in 16 of the 22 environmental predictors included in the final model. The variables contributing the most to the probability of modelled occurrence of *D. polymorpha* in Swedish lakes (according to the mean of importance across algorithms) are alkalinity (38 %) and proportion of agricultural land area (18 %), followed by proportion of mud (9%) and pH (8%). The remaining variables all explain 5% or less - proportion of open waters, proportion of wetlands, proportion of built-up areas, density of holiday homes, cumulated length of shorelines, total population, ammonium deposits, cumulative number of

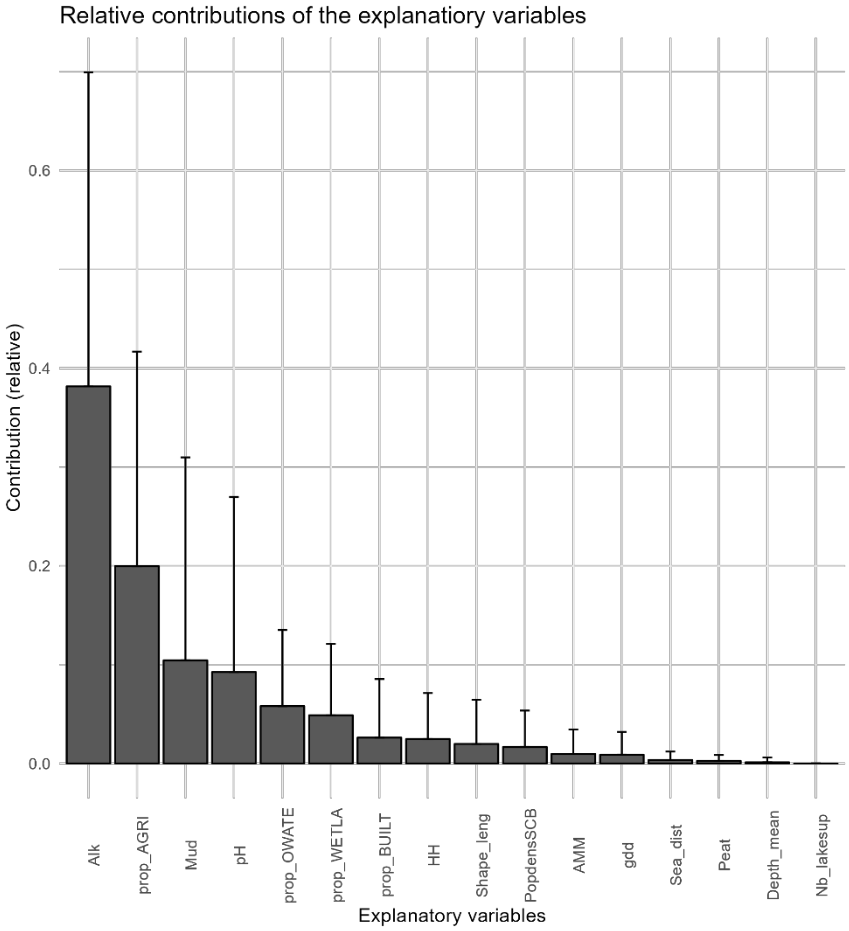

Figure 9: Relative contributions of explanatory variables for D. polymorpha. Alk - Alkalinity, prop_AGRI - proportion of agricultural land, Mud - proportion of mud, pH, prop_OWATE - proportion of open water, prop_WETLA - proportion of wet-lands, prop_BUILT - proportion of built area, HH - density of holiday homes, Shape_leng - lake shore length, PopdensSCB - population density, AMM – ammonium deposition, Gdd - length of growth season, Sea_dist distance to the sea, Peat- proportion of peat, Depth_mean - lake depth, Nb_lakesup - the number of lakes upstream.

degrees above 5°C, distance to the sea, proportion of peats, mean depth of the lake and number of lakes upstream (Fig. 9).

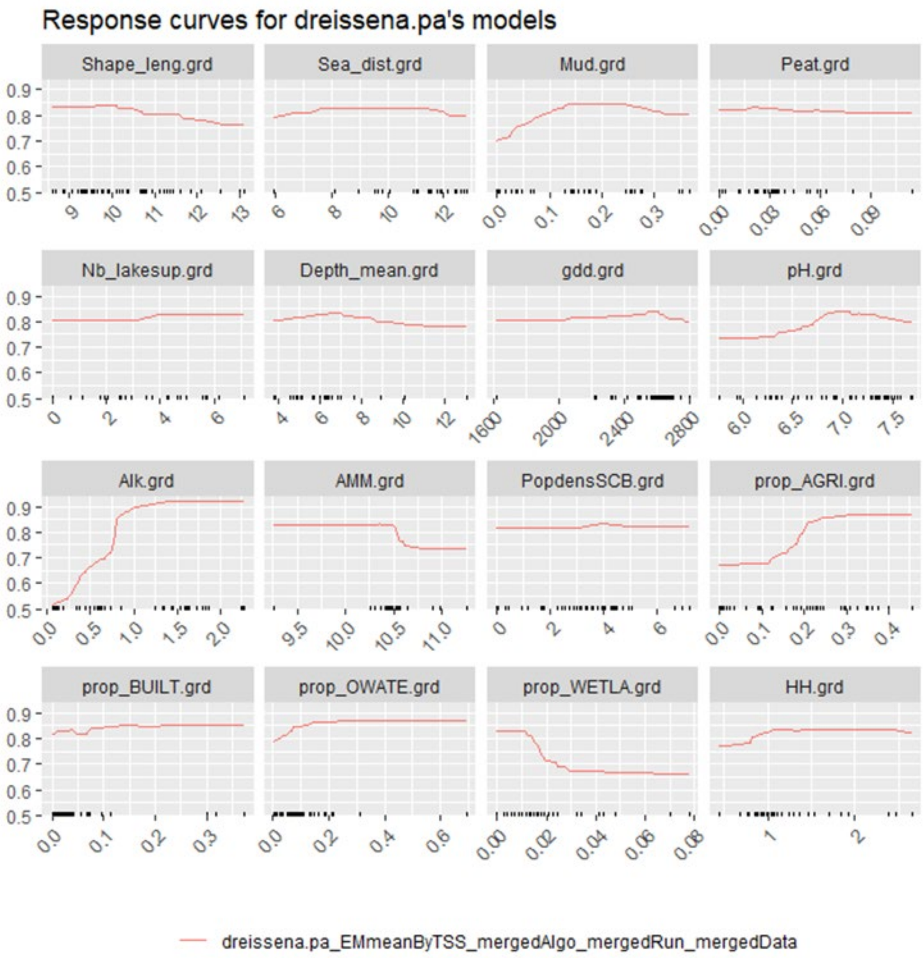

Figure 10: Modelled response curves for the environmental variables used in the ensemble model for D. polymorpha.

7.1.3 Projections based on environmental data

The ensemble probability of occurrence projection shows suitable habitats for the occurrence of *D. polymorpha* in many lakes across Sweden (Fig. 11). Lakes with probability of occurrence > 0.5 were concentrated in areas where *D. polymorpha* has been recorded: Uppsala and Stockholm County (mainly Lake Mälaren), part of Östergötland and Skåne County. The probability of occurrence map also underlines several lakes of high suitability in other regions where occurrences of *D. polymorpha* have not been recorded yet: Västra Götaland County, Östergötland County (including Lakes Vänern and Vättern), Jämtland County and the Island of Gotland. Thus, the results from this study suggest several areas across Sweden that need further study to determine if this invasive species is present or not and select several areas of high risk of colonisation if the species reaches the lakes.

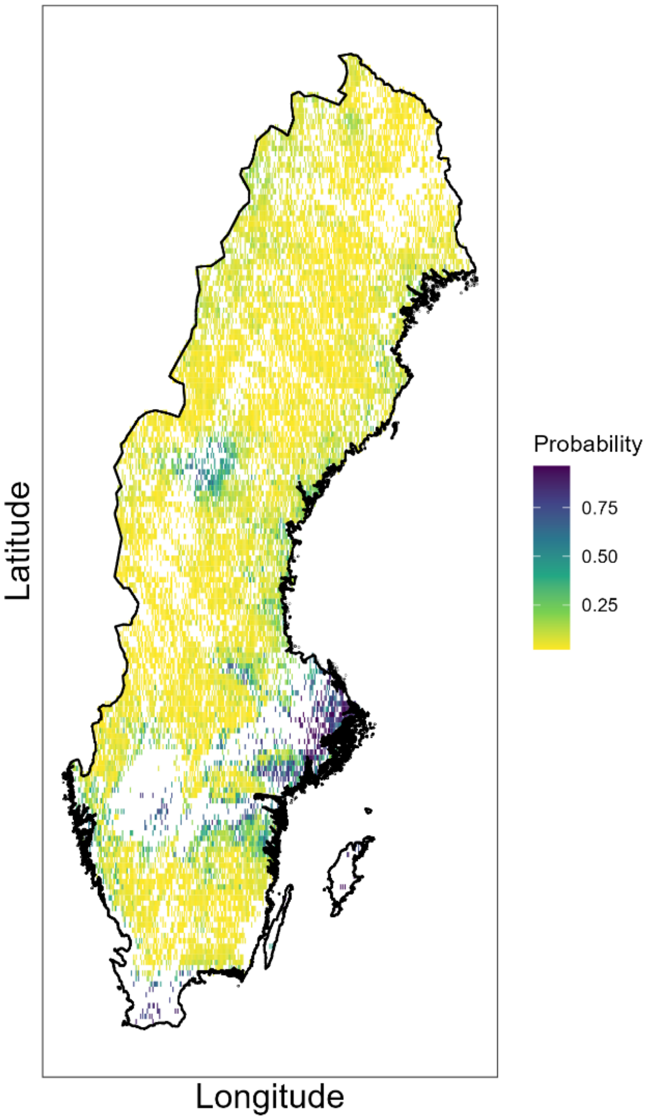

Figure 11: SDMs ensemble probability of occurrence projection for D. polymorpha in Swedish lakes. Purple colours show high probability of occurrence, while lighter shades of purple show intermediate probability of occurrence, and yellow colour shows a probability of occurrence, while lighter shades of purple show intermediate probability of occurrence, and yellow colour shows a probability of occurrence close to zero.

8 Discussion

Alkalinity was the main factor determining the high probability of occurrence of *D. polymorpha* in Sweden. Alkalinity is a measurement of the waters ability to buffer pH changes. Our model results show that above 0.5 meq/l the probability of *D. polymorpha* increase markedly (*D. polymorpha* requires at least 0.6 meq/l) (Fig. 10). This finding is not surprising, as with low alkalinity *D. polymorpha* would have more difficulties forming the calcium carbonate shells due to dissolution in low pH waters. Proportion of agricultural land was the second-best predictor determining the probability of occurrence of *D. polymorpha*. In fact, there is an increase of *D. polymorpha* probability of presence with an increase of the proportion of agricultural areas (Fig 10). These lakes are probably situated in catchments that are affected by land use such as agricultural and urbanization, resulting in elevated nutrients that favour phytoplankton proliferation, with an increase in food availability for this invasive bivalve. Areas with high probability of occurrence (> 0.5) were gathered in areas where *D. polymorpha* has already been recorded, particularly in big urban and agricultural areas around lake Mälaren, in Stockholm and Uppsala, in Östergötland and in Skåne County. However, the modelling indicates that favourable conditions occur in other parts of Sweden where *D. polymorpha* has not been detected yet: Västra Götaland (Lake Värnen and Vattern), parts of Östergötland, Kalmar, Jämtland and in Gotland. The areas of high probability of occurrence for *D. polymorpha* match with the study of Hallstan et al., (2010). Consequently, there is a high probability that *D. polymorpha* may increase its geographical distribution into this area. This result narrows down the number of lakes for specific monitoring efforts in search for this invasive bivalve and areas that may need information campaigns to the public to minimise unintentional introduction of this species.

Dispersal limitation is one of the main factors regulating the distribution and range expansion of a species. *D. polymorpha* overcome this obstacle thanks to its free-living veliger larvae stage that contribute to its high dispersal capacity and invasive behaviour (Goedkoop et al., 2021; Hallstan et al., 2010). However, the global expansion of *D. polymorpha* has been facilitated by human activities through global trade and recreational activities in connected water bodies. Even though *D. polymorpha* invasions have created socio-economical problem in the USA, costing millions of dollars in damage, its negative impacts have been less extensive in Europe (Hallstan et al., 2010). The establishment of zebra mussels, and subsequent retention of nutrients, has probably reduced the effects of eutrophication in numerous water bodies and resulted in increased water clarity instead, greatly reducing algal biomass and eutrophication (Goedkoop et al., 2021). Although the effects of the zebra mussel are not as extensive as in the US, it is important to closely monitor its ongoing range of expansion in Sweden. Authorities may need to start information campaigns to minimize the spread of *D. polymorpha* to other lakes via recreational activities (e.g., fishing gear and boats).

9 Future directions

A recent study from a large lake in Ireland (Crane *et al.*, 2022) confirmed earlier macrocosm findings (Crane *et al.*, 2020) of potentially important interactions between *E.nuttallii* and the invasive mussel *D.polymorpha*. The authors found a positive association between presences of the two species in the lake, and in macrocosm experiments found strongly enhanced *E.nuttallii* growth when *D.polymorpha* was present (but not the growth of *E.canadensis*). They suggest that when all three species co-occur (as is likely to be the case at an increasing number of locations in Sweden) the domination of *E.nuttallii* may be promoted. Certainly, as invasive species spread and come into contact to each other with greater frequency, more attention needs to be paid to interactions in future modelling work. Another potentially valuable direction, given the potential role of coastal populations in facilitating spread inland is combining marine and freshwater modelling.

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11 References

Abernethy, V. J., Sabbatini, M. R. & Murphy, K. J. (1996). Response of Elodea canadensis Michx, and Myriophyllum spicatum L. to shade, cutting and competition in experimental culture. *Hydrobiologia* [online], 340(1), pp. 219–224 Springer. Available from: https://doi.org/10.1007/BF00012758.

Alahuhta, J., Heino, J. & Luoto, M. (2011). Climate change and the future distributions of aquatic macrophytes across boreal catchments. *Journal of biogeography* [online], 38(2), pp. 383–393 Wiley. Available from: https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2699.2010.02412.x.

Aldridge, D. C., Elliott, P., & Moggridge, G. D. (2004). The recent and rapid spread of the zebra mussel (Dreissena polymorpha) in Great Britain. *Biological Conservation*, *119*(2), 253–261. https://doi.org/10.1016/J.BIOCON.2003.11.008

Allouche, O., Tsoar, A. & Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *The Journal of applied ecology* [online], 43(6), pp. 1223–1232 Wiley. Available from: https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2006.01214.x.

Angelstein, S. & Schubert, H. (2008). Elodea nuttallii: uptake, translocation and release of phosphorus. *Aquatic biology* [online], 3, pp. 209–216 Inter-Research Science Center. Available from: http://www.int-res.com/abstracts/ab/v3/n3/p209-216/.

Araújo, M. B. & New, M. (2007). Ensemble forecasting of species distributions. *Trends in ecology & evolution* [online], 22(1), pp. 42–47 Elsevier. Available from: http://dx.doi.org/10.1016/j.tree.2006.09.010.

Arwidsson I (1926) Vandraremusslan (Dreissensia polymorpha Pallas) inkommen i Sverige. Fauna och Flora 21:209–217

Barrat-Segretain, M.-H. (2004). Growth of Elodea canadensis and Elodea nuttallii in monocultures and mixture under different light and nutrient conditions. *Archiv fur Hydrobiologie* [online], 161(1), pp. 133–144 Schweizerbart. Available from: https://www.schweizerbart.de/papers/fal/detail/161/56212.

Best, E. P. H., Woltman, H. & Jacobs, F. H. H. (1996). Sediment-related growth limitation of Elodea nuttallii as indicated by a fertilization experiment. *Freshwater biology* [online], 36(1), pp. 33–44 Wiley. Available from: https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2427.1996.d01-474.x.

Bighiu, M. A., Norman Haldén, A., Goedkoop, W., & Ottoson, J. (2019). Assessing microbial contamination and antibiotic resistant bacteria using zebra mussels (Dreissena polymorpha). *Science of the Total Environment*, *650*, 2141–2149. https://doi.org/10.1016/J.SCITOTENV.2018.09.314

Bowman, M. F., & Bailey, R. C. (1998). Upper pH tolerance limit of the zebra mussel (Dreissena polymorpha) . *Canadian Journal of Zoology*, *76*(11), 2119–2123. https://doi.org/10.1139/z98-155

Bowmer, K. H., Jacobs, S. W. L. & Sainty, G. R. *Identification, Biology and Management of Elodea canadensis, Hydrocharitaceae*. [online] (1995). Available from: https://www.apms.org/wp-content/uploads/japm-33-01-013.pdf.

Brandrud, T. E. & Mjelde, M. *Vasspest (Elodea canadensis) Effekter på biologisk mangfold. Spredningsmønstre og tiltak*. [online] (1999). Available from: https://niva.brage.unit.no/niva-xmlui/handle/11250/210463.

Breiman, L. (2001). Random Forests. *Machine learning* [online], 45(1), pp. 5–32. Available from: https://doi.org/10.1023/A:1010933404324.

Breiman, L. & Ihaka, R. (1984). *Nonlinear discriminant analysis via scaling and ACE* [online]. Department of Statistics, University of California Davis One Shields Avenue …. Available from: https://digitalassets.lib.berkeley.edu/sdtr/ucb/text/40.pdf.

Clayton, J. & Edwards, T. (2006). Aquatic plants as environmental indicators of ecological condition in New Zealand lakes. In: Caffrey, J. M., Dutartre, A., Haury, J., Murphy, K. J., & Wade, P. M. (Eds.) *Macrophytes in Aquatic Ecosystems: From Biology to Management: Proceedings of the 11th International Symposium on Aquatic Weeds, European Weed Research Society*. pp. 147–151. Dordrecht: Springer Netherlands. ISBN 9781402053900.

Crane, K., Coughlan, N. E., Cuthbert, R. N., Dick, J. T. A., Kregting, L., Ricciardi, A., MacIsaac, H. J. & Reid, N. (2020). Friends of mine: An invasive freshwater mussel facilitates growth of invasive macrophytes and mediates their competitive interactions. *Freshwater biology* [online], 65(6), pp. 1063–1072 Wiley. Available from: https://onlinelibrary.wiley.com/doi/10.1111/fwb.13489.

Crane, K., Kregting, L., Coughlan, N. E., Cuthbert, R. N., Ricciardi, A., MacIsaac, H. J., Dick, J. T. A. & Reid, N. (2022). Abiotic and biotic correlates of the occurrence, extent and cover of invasive aquatic Elodea nuttallii. *Freshwater biology* [online], 67(9), pp. 1559–1570. Available from: http://dx.doi.org/10.1111/fwb.13960.

Dendène, M. A., Rolland, T., Trémolières, M. & Carbiener, R. (1993). Effect of ammonium ions on the net photosynthesis of three species of Elodea. *Aquatic botany* [online], 46(3), pp. 301–315 Elsevier. Available from: https://www.sciencedirect.com/science/article/pii/030437709390010T.

van Donk, E., Gulati, R. D., Iedema, A. & Meulemans, J. T. (1993). Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake. In: Hillbricht-Ilkowska, A. & Pieczyńska, E. (Eds.) *Nutrient Dynamics and Retention in Land/Water Ecotones of Lowland, Temperate Lakes and Rivers*. pp. 19–26. Dordrecht: Springer Netherlands. ISBN 9789401116022.

European Union, Copernicus Land Monitoring Service (2018), European Environment Agency (EEA)

Friedman, J. H. (1991). *Estimating functions of mixed ordinal and categorical variables using adaptive splines* [online]. Stanford Univ CA Lab for Computational Statistics.

Gillard, M., Thiébaut, G., Deleu, C. & Leroy, B. (2017). Present and future distribution of three aquatic plants taxa across the world: decrease in native and increase in invasive ranges. *Biological invasions* [online], 19(7), pp. 2159–2170 Springer. Available from: https://doi.org/10.1007/s10530-017-1428-y.

Goedkoop, W., Choudhury, M. I., Lau, D. C. P., & Grandin, U. (2021). Inverting nutrient fluxes across the land-water interface – Exploring the potential of zebra mussel (Dreissena polymorpha) farming. *Journal of Environmental Management*, *281*(August 2020), 111889. https://doi.org/10.1016/j.jenvman.2020.111889

Hallstan, S., Grandin, U., & Goedkoop, W. (2010). Current and modeled potential distribution of the zebra mussel (Dreissena polymorpha) in Sweden. *Biological Invasions*, *12*(1), 285–296. https://doi.org/10.1007/s10530-009-9449-9

Hanley, J. A. & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* [online], 143(1), pp. 29–36 pubs.rsna.org. Available from: http://dx.doi.org/10.1148/radiology.143.1.7063747.

Hastie, T. & Tibshirani, R. (1990). Exploring the nature of covariate effects in the proportional hazards model. *Biometrics* [online], 46(4), pp. 1005–1016 JSTOR. Available from: https://www.ncbi.nlm.nih.gov/pubmed/1964808.

Hastie, T., Tibshirani, R. & Buja, A. (1994). Flexible Discriminant Analysis by Optimal Scoring. *Journal of the American Statistical Association* [online], 89(428), pp. 1255–1270 Taylor & Francis. Available from: https://doi.org/10.1080/01621459.1994.10476866.

Hessen, D. O., Skurdal, J. & Braathen, J. E. (2004). Plant Exclusion of a Herbivore; Crayfish Population Decline caused by an Invading Waterweed. *Biological invasions* [online], 6(2), pp. 133–140 Springer. Available from: https://doi.org/10.1023/B:BINV.0000022131.40783.f0.

Hincks, S. S., & Mackie, G. L. (1997). *Effects of pH, calcium, alkalinity, hardness, and chlorophyll on the survival, growth, and reproductive success of zebra mussel (Dreissena polymorpha) in Ontario lakes*.

Hosler, D. M. (2011). Early detection of dreissenid species: Zebra/Quagga mussels in water systems. *Aquatic Invasions*, *6*(2), 217–222. https://doi.org/10.3391/ai.2011.6.2.10

Jones, J. I., Eaton, J. W. & Hardwick, K. (1993). Physiological plasticity in Elodea nuttallii (Planch.) St. John. *Journal of aquatic plant management* [online], 31, pp. 88–88 AQUATIC PLANT MANAGEMENT SOCIETY INC. Available from: https://apps.dtic.mil/sti/pdfs/ADA275535.pdf#page=102.

Josefsson, M. & Andersson, B. (2001). The environmental consequences of alien species in the Swedish lakes Mälaren, Hjälmaren, Vänern and Vättern. *Ambio* [online], 30(8), pp. 514–521 BioOne. Available from: http://dx.doi.org/10.1579/0044-7447-30.8.514.

Karatayev, A.Y., Burlakova, L. E., & Padilla, D. K. (2002). and Their Role As Ecosystem Engineers. *Invasive Aquatic Species of Europe*, 433–434.

Karatayev, Alexander Y., Boltovskoy, D., Padilla, D. K., & Burlakova, L. E. (2007). The invasive bivalves Dreissena polymorpha and Limnoperna fortunei: Parallels, contrasts, potential spread and invasion impacts. *Journal of Shellfish Research*, *26*(1), 205–213. https://doi.org/10.2983/0730-

8000(2007)26[205:TIBDPA]2.0.CO;2

Karatayev, Alexander Y., Burlakova, L. E., & Padilla, D. K. (1997). The effects of dreissena polymorpha (Pallas) invasion on aquatic communities in eastern Europe. *Journal of Shellfish Research*, *16*(1), 187–203.

Kunii, H. (1981). Characteristics of the winter growth of detached Elodea nuttallii (Planch.) St. John in Japan. *Aquatic botany* [online], 11, pp. 57–66 Elsevier. Available from: https://www.sciencedirect.com/science/article/pii/0304377081900462.

Kunii, H. (1984). Seasonal growth and profile structure development of Elodea nuttallii (Planch.) St. John in pond Ojaga-Ike, Japan. *Aquatic botany* [online], 18(3), pp. 239–247 Elsevier. Available from: https://www.sciencedirect.com/science/article/pii/0304377084900652.

Larson, D. (2003). *Predicting the threats to ecosystem function and economy of alien vascular plants in freshwater environments* [online]. Sveriges lantbruksuniv. Available from: http://info1.ma.slu.se/ima/publikationer/internserie/2003-07.pdf.

Larson, D. & Willén, E. (2007). The relationship between biodiversity and invasibility in central Swedish lakes invaded by Elodea species. In: Gherardi, F. (Ed.) *Biological invaders in inland waters: Profiles, distribution, and threats*. pp. 423–433. Dordrecht: Springer Netherlands. ISBN 9781402060298.

Lindim, C. (2015). Modeling the impact of Zebra mussels (Dreissena polymorpha) on phytoplankton and nutrients in a lowland river. *Ecological Modelling*, *301*, 17–26. https://doi.org/10.1016/j.ecolmodel.2015.01.012

Lodge, D. M. (1991). Herbivory on freshwater macrophytes. *Aquatic botany* [online], 41(1), pp. 195–224 , Elsevier. Available from: https://www.sciencedirect.com/science/article/pii/0304377091900446.

McCullagh, P. & Nelder, J. A. (1989). [CITAT] Binary data. *Generalized linear models*, Springer.

Mackie, G. L. (1991). Biology of the exotic zebra mussel, Dreissena polymorpha, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia*, *219*(1), 251–268. https://doi.org/10.1007/BF00024759

Marsden, J. E. (2011). Standard protocols for monitoring and sampling zebra mussels. *Standard Protocols for Monitoring and Sampling Zebra Mussels*. https://doi.org/10.5962/bhl.title.15187

McMahon, R. F., & Bogan, A. E. (n.d.). MOLLUSCA: BIVALVIA. In *Ecology and Classification of North American Freshwater Invertebrates* (Second Edi). ACADEMIC PRESS. https://doi.org/10.1016/B978-0-12-690647-9.50012-0

Mei, X., Zhang, X., Kassam, S. S., & Rudstam, L. G. (2016). Will the displacement of zebra mussels by quagga mussels increase water clarity in shallow lakes during summer? Results from a mesocosm experiment. *PLoS ONE*, *11*(12), 1–15. https://doi.org/10.1371/journal.pone.0168494

Mielecki, M. & Pieczynska, E. (2005). The influence of fragmentation on the growth of Elodea canadensis Michx. in different light conditions. *Polish Journal of Ecology* [online], 2(53) infona.pl. Available from: https://www.infona.pl/resource/bwmeta1.element.agro-article-61809d9c-931d-47fb-9d8f-3d30909d116a.

Mjelde, M., Lombardo, P., Berge, D. & Johansen, S. W. (2012). Mass invasion of non-nativeElodea canadensisMichx. in a large, clear-water, species-rich Norwegian lake – impact on macrophyte biodiversity. *Annales de limnologie* [online], 48(2), pp. 225–240 EDP Sciences. Available from: https://www.cambridge.org/core/journals/annales-de-limnologie-international-journal-of-limnology/article/mass-invasion-of-nonnative-elodea-canadensis-michx-in-a-large-clearwater-speciesrich-norwegian-lake-impact-on-macrophyte-biodiversity/4C250B2CD747F1788A6F9A851679F092.

Naddafi, R., Blenckner, T., Eklöv, P., & Pettersson, K. (2011). Physical and chemical properties determine zebra mussel invasion success in lakes. *Hydrobiologia*, *669*(1), 227–236. https://doi.org/10.1007/s10750-011-0689-1

Nino, F. D., Thiébaut, G. & Muller, S. (2005). Response of Elodea Nuttallii (Planch.) H. St. John to Manual Harvesting in the North-East of France. *Hydrobiologia* [online], 551(1), pp. 147–157 Springer. Available from: https://doi.org/10.1007/s10750-005-4457-y.

Peterson, A. T. & Vieglais, D. A. (2001). Predicting species invasions using ecological niche modeling: New approaches from bioinformatics attack a pressing problem. *Bioscience* [online], 51(5), p. 363 Oxford University Press (OUP). Available from: https://academic.oup.com/bioscience/article-abstract/51/5/363/243986. [Accessed 2023-01-13].

Pollux, B. J. A., Velde, G. Van Der, & Vaate, A. De. (2022). *A perspective on global spread of Dreissena polymorpha: a review on possibilities and limitations*.

Ridgeway, G. *The state of boosting*. [online] (1999). Available from: http://www.planchet.net/EXT/ISFA/1226.nsf/0/a29acbd26d902d6fc125822a0031c09b/$FILE/boosting.pdf. [Accessed 2023-01-13].

Ripley, B. D. (2007). *Pattern Recognition and Neural Networks* [online]. Cambridge University Press. Available from: https://play.google.com/store/books/details?id=m12UR8QmLqoC.

Sand-Jensen, K., Riis, T., Vestergaard, O. & Larsen, S. E. (2000). Macrophyte decline in Danish lakes and streams over the past 100 years. *The Journal of ecology* [online], 88(6), pp. 1030–1040 Wiley. Available from: https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2745.2000.00519.x.

Segurado, P. & Araújo, M. B. (2004). An evaluation of methods for modelling species distributions. *Journal of biogeography* [online], 31(10), pp. 1555–1568 Wiley. Available from: https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2699.2004.01076.x.

Simpson, D. A. *(Planch.) H. st John in the British isles*. [online] (1990). Available from: http://archive.bsbi.org.uk/Wats18p173.pdf.

Simpson, D., Benedictow, A., Berge, H., Bergström, R., Emberson, L. D., Fagerli, H., Flechard, C. R., Hayman, G. D., Gauss, M., Jonson, J. E., Jenkin, M. E., Nyíri, A., Richter, C., Semeena, V. S., Tsyro, S., Tuovinen, J.-P., Valdebenito, Á., and Wind, P.: The EMEP MSC-W chemical transport model – technical description, Atmos. Chem. Phys., 12, 7825–7865, https://doi.org/10.5194/acp-12-7825-2012, 2012.

Simpson, D., Bergström, Tsyro, S., and Wind, P.: Updates to the EMEP MSC-W model, 2019–2020, in: Transboundary particulate matter, photo-oxidants, acidifying and eutrophying components. EMEP Status Report 1/2020, pp. 155–165, The Norwegian Meteorological Institute, Oslo, Norway.

Sprung, M. 1987. Ecological requirements of developing Dreissena polymorpha eggs. Arch. Hydrobiol. Suppl. 79: 69–86

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science* [online], 240(4857), pp. 1285–1293 science.org. Available from: http://dx.doi.org/10.1126/science.3287615.

Thuiller, W. (2003). BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. *Global change biology* [online], 9(10), pp. 1353–1362 Wiley. Available from: https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2486.2003.00666.x.

Thuiller W, Georges D, Gueguen M, Engler R, Breiner F, Lafourcade B, Patin R (2022). biomod2: Ensemble Platform for Species Distribution Modeling. R package version 4.2-1.

Warziniack, T., Haight, R. G., Yemshanov, D., Apriesnig, J. L., Holmes, T. P., Countryman, A. M., Rothlisberger, J. D., & Haberland, C. (2021). Economics of Invasive Species. *Invasive Species in Forests and Rangelands of the United States*, 305–320. https://doi.org/10.1007/978-3-030-45367-1_14

Werner, S., Mörtl, M., Bauer, H. G., & Rothhaupt, K. O. (2005). Strong impact of wintering waterbirds on zebra mussel (Dreissena polymorpha) populations at Lake Constance, Germany. *Freshwater Biology*, *50*(8), 1412–1426. https://doi.org/10.1111/j.1365-2427.2005.01411.x

Whittier, T. R., Ringold, P. L., Herlihy, A. T., & Pierson, S. M. (2008). A calcium-based invasion risk assessment for zebra and quagga mussels (Dreissena spp). *Frontiers in Ecology and the Environment*, *6*(4), 180–184. https://doi.org/10.1890/070073

12 Appendix 1: Rasters of explanatory variables