Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Institutionen för vatten och miljö

Modelling the risks of *Nymphoides peltata* spread in Swedish lakes

James Weldon

SLU, Vatten och miljö: Rapport 2024:15

Cover photo: Nymphoides peltata, CC BY-SA4.0 licence

Publication: Digital only

Publication year: 2024

DOI: https://doi.org/10.54612/a.nmtj4tgmer

Contact:

james.weldon@slu.se

http://www.slu.se/vatten-miljo

https://orcid.org/0000-0002-3802-4177

Code available from Github: https://github.com/JWeld/Nymphoides_SDM

Rapporten har tagits fram på uppdrag av Havs- och vattenmyndigheten. Rapportförfattarna ansvarar för innehållet och slutsatserna i rapporten. Rapportens innehåll innebär inte något ställningstagande från Havs- och vattenmyndighetens sida.

Updated version. This pdf was updated 2024-12-06. Figure 5 on p16 (section 3.1.12) was previously missing labels on the species response curves

Institutionen för vatten och miljö, SLU
Box 7050, SE-750 07 Uppsala, Sweden
Org.nr 202100-2817
tel: +46 (0)18-67 10 00
www.slu.se/vatten-miljo

Contents

Summary (English and Swedish)

Species distribution modelling is a valuable tool for identifying areas most at risk of the spread of potentially harmful species. Here we model the environmental factors governing the distribution of a harmful species of concern that is currently found in Sweden at only a limited number of locations: the aquatic macrophyte *N. peltata* (sjögull). The most important factors determining risk of establishment are water chemistry (sufficient amounts of calcium is required), temperature (the species is partly limited by colder temperatures in Sweden) and connectivity to other water bodies. The results how that there are potentially a large number of lakes in mid to southern Sweden where *N. peltata* could establish populations, with undesirable consequences for biodiversity and recreation.

Modellering är ett värdefullt verktyg för att identifiera områden som löper störst risk för spridning av potentiellt skadliga arter. Här modellerar vi de miljöfaktorer som styr utbredningen av en skadlig art som orsakar bekymmer, och som för närvarande endast finns på ett begränsat antal platser i Sverige: den akvatiska makrofyten *N. peltata* (sjögull). De viktigaste faktorerna som avgör risken för etablering är vattenkemi (tillräckligt med kalcium krävs), temperatur (arten begränsas delvis av kallare temperaturer i Sverige) och konnektiviteten till andra vatten. Resultaten visar att det finns potentiellt ett stort antal sjöar i mellersta till södra Sverige där *N. peltata* skulle kunna etablera populationer, med oönskade konsekvenser för biologisk mångfald och rekreation.

Institutionen för vatten och miljö, SLU
Box 7050, SE-750 07 Uppsala, Sweden
Org.nr 202100-2817
tel: +46 (0)18-67 10 00
www.slu.se/vatten-miljo

1 *Nymphoides peltata* - 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 potentially harmful 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.

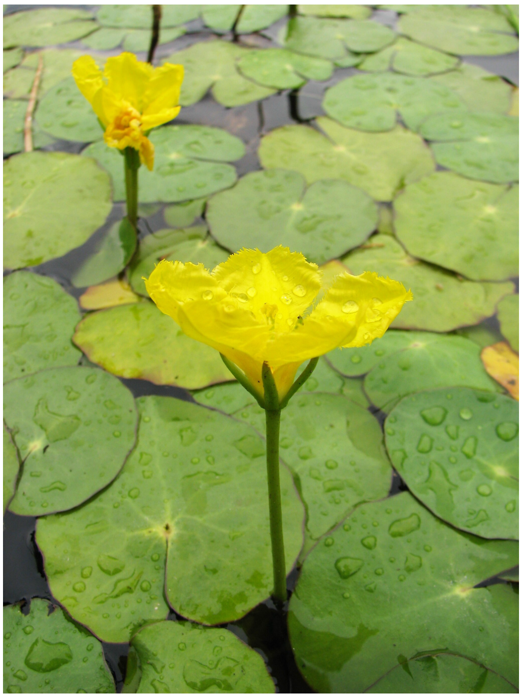

Figure 1: "Nymphoides peltata Grzybieńczyk wodny 2010-06-20 03" by Agnieszka Kwiecień, Nova is licensed under CC BY-SA 4.0.

We focus in this report on *Nymphoides peltata*, (sjögull in Swedish), an aquatic macrophyte not native to Sweden whose spread is associated with harmful ecological and social effects. *N. peltata* has a native range from China and Japan to western Asia and central Europe but has been introduced to other areas as an ornamental species due to its attractive yellow flowers. It was first introduced to Sweden in this context as far back as the 1870s and can now be found in ca. 40 lakes and water courses in southern and mid-Sweden. The potential for spread in Lake

Mälaren has been especially noted and a 2019 inventory (Stenmark *et al.*, 2020) found the species at 14 locations, with a total of 83 colonies.

The species is problematic as it forms dense mats of floating leaves that displace other macrophytes (and any other species that depend on them), cause low light conditions beneath them, hinder boat traffic, and can make lakes unsuitable for recreational activities such as swimming and fishing. These stands also decay in the winter, resulting in a rapid release of nutrients that can negatively impact water quality and biodiversity.

Objectives of the study

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

1.1 *N. peltata's* environmental niche

Depth and flow

N. peltata is found in lakes and slow flowing rivers in relatively shallow water, up to a depth of around 3 meters.

Nutrients and water chemistry

N. peltata thrives best in eutrophic, alkaline, high pH waters. Alkaline water has a higher dissolved calcium availability, which is used by *N. peltata* in leaf development (van der Velde et al., 1986). The species' optimum alkalinity appears to be around 3.75 meq l^{-1}, (Smits et al., 1988) but it can be found at considerably lower levels. However, transplantation experiments indicated that calcium availability is the key limiting factor rather than alkalinity per se (Smits *et al.*, 1992) and that, at least in the Netherlands, the species was not found where Ca was less than 0.24 meq l^{-1}

Temperature

Growth of *N. peltata* occurs most of the year except during their overwintering dormant period (which in Sweden is relatively long approximately December to May). The northern distribution limit in Europe has previously been described as roughly corresponding to the 16 °C July isotherm (van der Voo & Westhoff, 1961), which corresponds well with its distribution in Sweden. *N. peltata*'s natural range includes areas in west Asia and eastern Europe with cold winters, and winter conditions in at least the southern third of Sweden are evidently no obstacle to establishment.

1.2 Reproduction and lifecycle

N. peltata is able to reproduce both sexually and vegetatively, however genetic analysis of plants in Sweden (Larson, 2007) showed a low variation that indicates vegetative reproduction is the dominant method here. This is unfortunately not a serious limitation on spread as small plant fragments can be dispersed downstream and form roots and start growing. Theoretically, water birds can act as a transport vector between unconnected water bodies (Sand-Jensen *et al.*, 2000), as can the movement of small recreational boats between lakes. Mechanical removal of biomass as a control method also risks creating small fragments that can travel and spread the species further.

1.3 Impact of *N. peltata*

1.3.1 Ecological impacts

N. peltata is a strong competitor, and can displace the native macrophyte community (Darbyshire & Francis, 2008) as it grows rapidly and forms dense floating mats of leaves that can monopolise the supply of light, and nutrients. Conditions may also become unsuitable for various animal species such as fish and insects as a result. *N. peltata* is sediment rooted, and transfers nutrients to the above-ground parts of the plant. The subsequent decomposition of large volumes of plant matter when *N. peltata* goes into its winter dormancy period can cause issues with oxygen depletion and oversupply of nutrients (Smålander & Olsson, 2020).

1.3.2 Economic / social impacts

Dense floating mats of *N. peltata* make water bodies unsuitable for a range of recreation activities such as bathing, fishing and boating. These negative impacts motivate attempts to control or eradicate *N. peltata* locally, which are costly and have had only a mixed record of success.

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.

R code for models is available from GitHub: https://github.com/JWeld/Nymphoides_SDM

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) *N. peltata data*
    - Occurrence data collected from two different sources:
        - National macrophytes inventory program between 2007 and 2024, 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 2000-2024 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.
    - *N. peltata* 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).

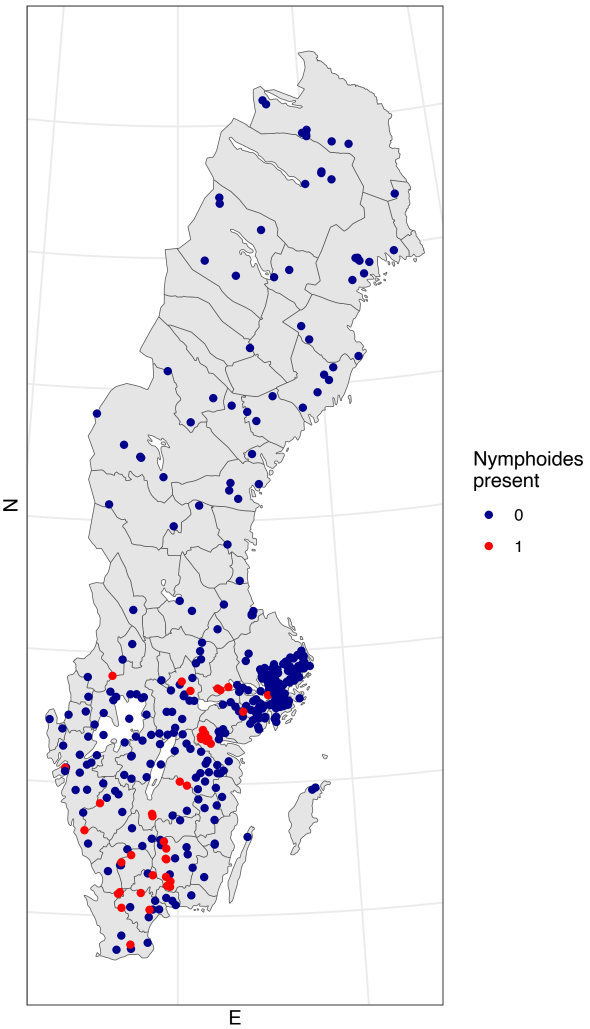

Figure 2 Observations and confirmed absences of N. peltata, matched to a lake

3) Environmental data/ explanatory variables

An initial selection of environmental factors was based on a literature review on the ecological preferences of *N. peltata* and other freshwater macrophytes (e.g., Bornette & Puijalon 2011, Buchan & Paddilla 2000, Son et al. 2017).

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 > 5), and a stepwise procedure of removing the variable with the highest VIF until all remaining variables have a VIF < 5 was used to produce a final list of explanatory variables. While this is an essential step there is an unavoidable inclusion of variables which are somewhat correlated as so many environmental variables in Sweden follow a strong north-south gradient. The following categories and variables were included in the final models after this selection process:

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 *N. peltata* growth is depth limited.
- Mud: proportion of moraine and silt within catchment
- Cumulative length of shorelines: total length of shorelines for each water surface, including islands within lakes (as shallow waters are suitable habitats for *N. peltata*).

Connectivity:

- Number of lakes upstream: measured using the stream network and connectivity between lakes (SMHI).

Water chemistry/quality:

- 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 *N. peltata*. The proportion of agricultural areas was derived from the CORINE (European Union, 2018) land cover at a resolution of 250 x 250 m.
- pH. Spatial interpolation of measured pH for 5709 lakes. Provided by Omdrevssjöar database, Institutionen för Vatten och Miljö (SLU).
- Calcium. Spatial interpolation of measured pH for 5709 lakes. Provided by Omdrevssjöar database, Institutionen för Vatten och Miljö (SLU).

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 *N. peltata*.

Human impacts:

- Human population density. Population density data from SCB (Statistiska centralbyråns, Statistics Sweden) at 1 x 1 km resolution.

Climate:

- Number of growing degree days above 5°C.
- A categorical variable for the temperature boundary indicated in the literature (see section 1.1)

Variables were in most cases log transformed before use in modelling. 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 (including 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 (ROC) (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 - ROC values is a useful guideline when reading modelling results such as these (Swets, 1988): Value>0.9: excellent agreement between observed and predicted distribution; 0.8<Value<0.9: good model accuracy; 0.7<Value<0.8: fair; 0.6<Value<0.7: poor; Value<0.6: fail.

3 Results

3.1 Results of ensemble modelling

3.1.1 Predictive performance of the models

For the models used the two measures, for quantification of how well the model distinguishes presences from absences showed that the mean TSS is 0.66, and the mean AUC ROC is of 0.86. The models can therefore be classified as having good accuracy, although they do not perfectly predict the distribution of *N. peltata*. As expected, the AUC ROC and TSS scores are somewhat variable, depending on the modelling method used (Fig. 3). Model RF was excluded for clear overfitting, while SRE and XGBoost do not work well with categorical variables. Note that when included in the ensemble model, contributions are performance weighted and models with predictive performance under TSS 0.6 and AUC ROC 0.8 are excluded from the ensemble model.

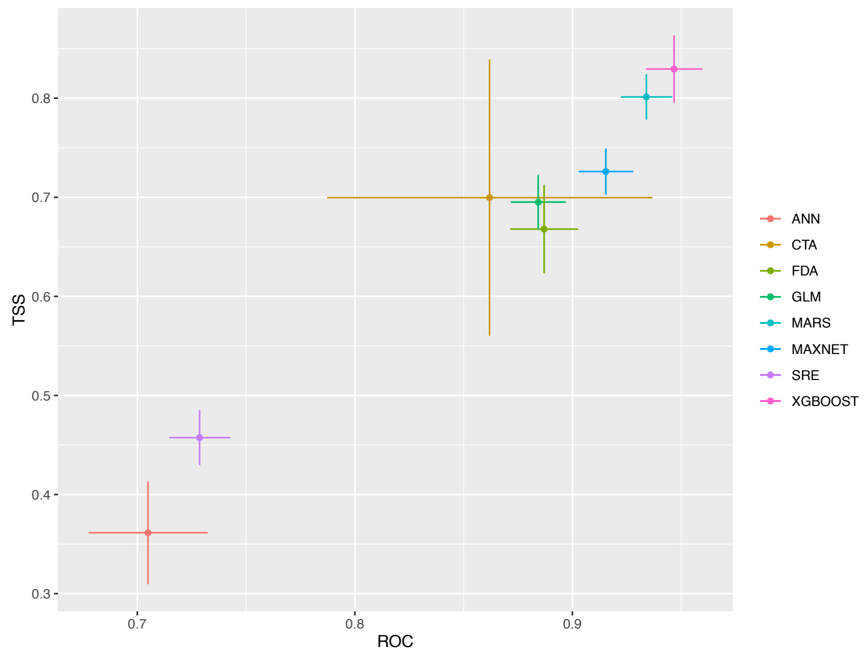

Figure 3: TSS and ROC values for each statistical method used (30 replicates) for N.peltata.

3.1.2 Variable importance

The variables contributing the most to the probability of modelled occurrence of *N. peltata* in Swedish lakes (according to the mean of importance across algorithms) are calcium availability (37%), temperature limit (16%), the number of lakes upstream (15 %) and pH (9%). The remaining variables all explain 5% or less – growth season length, lake depth, mud, proportion of agricultural land/open water, population density and lake edge length. (Fig. 4).

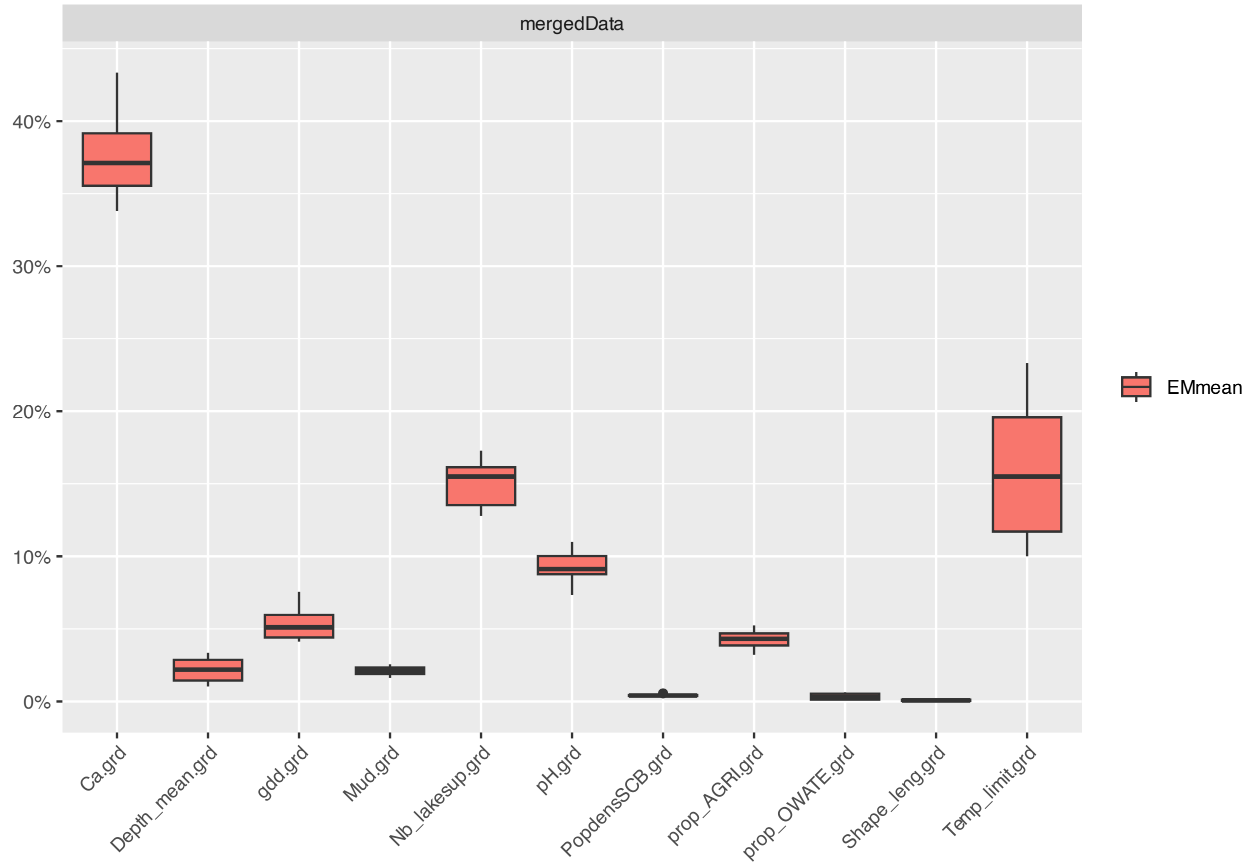

Figure 4: Relative contributions of explanatory variables for N. peltata. Ca- calcium level, Depth_mean - lake depth, gdd – length of growing season, Mud- proportion of mud, Nb_lakesup - the number of lakes upstream, pH, PopdensSCB – human population density, prop_AGRI - proportion of agricultural land, prop_OWATE - proportion of open water, Shape_leng - lake shore length, Temp_limit – categorical variable for temperature tolerance boundary.

The response curves for the explanatory variables, shown in Fig. 5, largely reflect the importance shown in Fig. 4. The temperature response shows a sharp boundary rather than a smooth gradient, while there is a clear optimum for calcium availability (around 0.3 meq l^{-1} when not log transformed). The decline at higher Ca levels however is likely to reflect the fact that many alkaline/ high Ca lakes in Sweden are found in areas that are too cold for this species. A gradual increase in probability of occurrence can be seen with increasing agricultural cover (i.e. linked to nutrient levels), mud and number of lakes upstream (connectivity). Experimenting with various model setups with roughly equivalent predictive performance indicated that the variables identified as most important are stable, although the role of temperature may be allocated differently between length of growing season and temperature tolerance boundary (these are the two variables with the highest correlation included in the model).

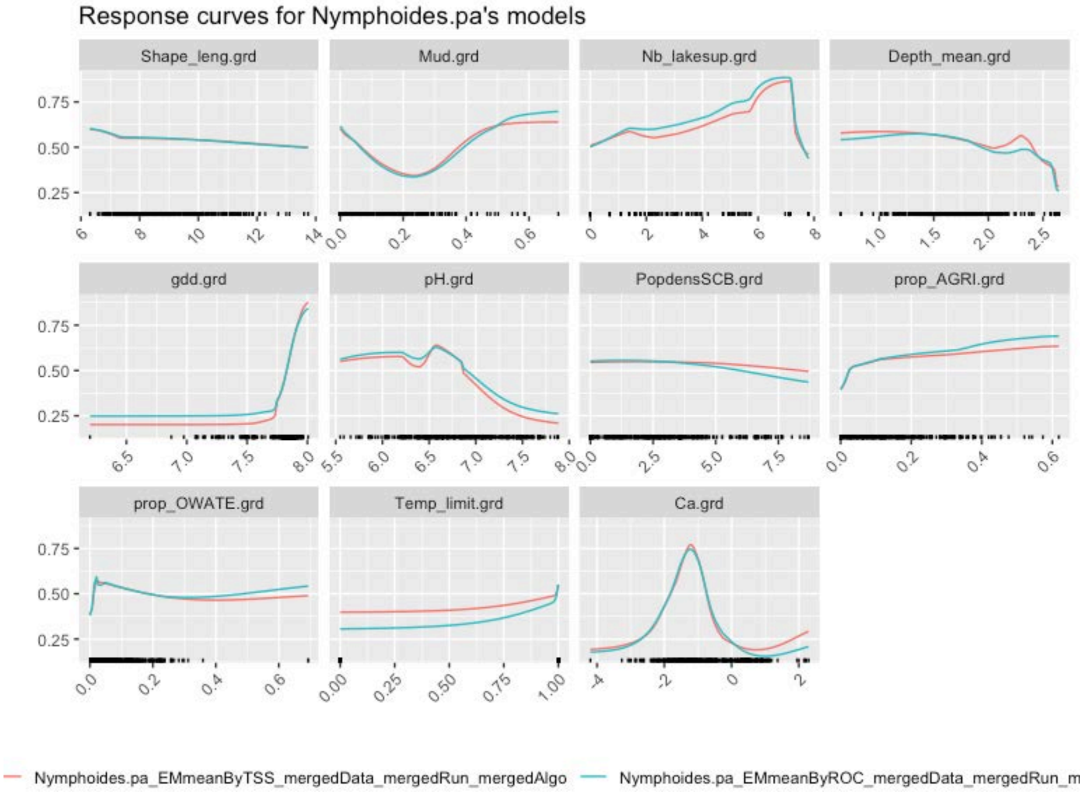

Figure 5: Modelled response curves for the environmental variables used in the ensemble model for N. peltata. Note that variables are transformed (log or log +1), except pH (untransformed) and Temp_limit (categorical).

3.1.3 Projections based on environmental data

The modelled projection of probability of occurrence is shown in Fig. 6. The temperature tolerance boundary is reflected in low probabilities north of the current observations, although some more northerly areas may be within the species limits such as areas of Gävleborgs county near the coast. Where temperature is not a limiting factor, areas of high and lower probability seem to be determined by pH/calcium, with areas of higher acidity at lower risk.

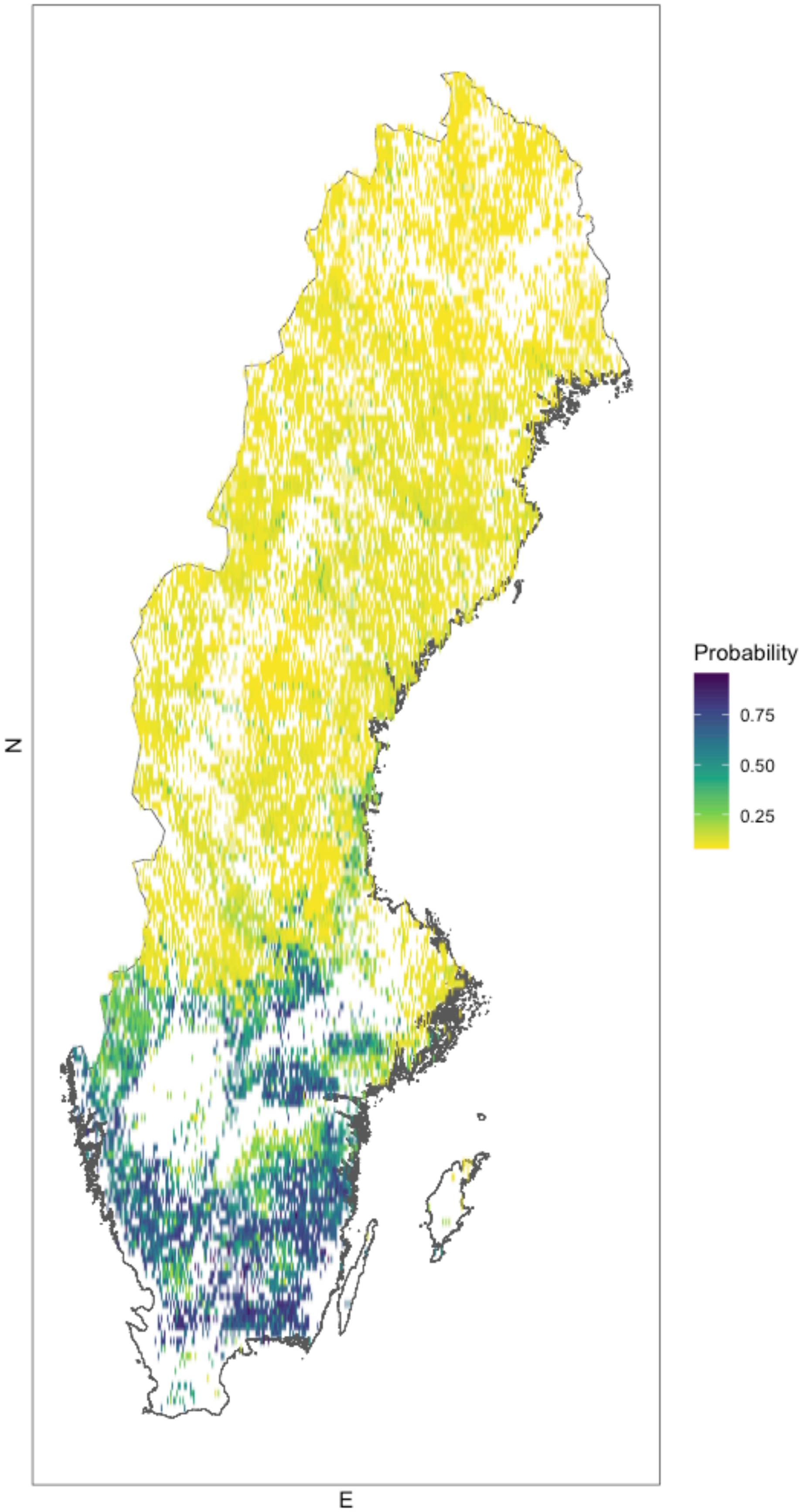

Figure 6: Modelled probability of N. peltata in Swedish lakes.

4 Conclusion

The current distribution of *N. peltata* in Swedish lakes is limited to lakes in the southern third of the country (Fig. 2), due to temperature constraints. Our modelling suggests that temperature, water chemistry in terms of calcium and pH, and level of interconnectivity with other lakes are the most important environmental variables for a high probability of *N. peltata* presence. This results in a large number of lakes in the southern parts of Sweden that are potential habitats for *N. peltata* (Fig. 6), although within this zone there are also areas where acidity (natural, or due to deposition and forestry practices) is an obstacle to its establishment. Where lake liming is undertaken in lakes connected to water bodies with *N. peltata* colonies it may be worth considering if liming is also creating suitable habitat for this problematic species. While inland areas much north of the current distribution are probably too cold, there are areas where the milder climate near the coast could potentially facilitate establishment. Given the strong role of temperature limitation for *N. peltata* establishment in Sweden, an obvious long-term concern is that climate change will put more areas at risk in the future.

5 Acknowledgements

Thanks are due to Stina Drakare (SLU) for comments, and to the Swedish Agency for Marine and Water Management (HaV) for funding this study.

6 References

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.

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.

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.

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.

Darbyshire, S. J. & Francis, A. (2008). The biology of invasive alien plants in Canada. 10. Nymphoides peltata (S. g. gmel.) Kuntze. *Canadian journal of plant science* [online], 88(4), pp. 811–829 Canadian Science Publishing. Available from: https://cdnsciencepub.com/doi/10.4141/CJPS07208. [Accessed 2024-10-31].

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.

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.

Larson, D. (2007). Reproduction strategies in introduced Nymphoides peltata populations revealed by genetic markers. *Aquatic botany* [online], 86(4), pp. 402–406 Elsevier BV. Available from: http://dx.doi.org/10.1016/j.aquabot.2006.11.009. [Accessed 2024-10-31].

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

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].

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.

Smålander, A. & Olsson, P. (2020). *BEKÄMPNING AV SJÖGULL (NYMPHOIDES PELTATA) INOM MÖRRUMSÅNS AVRINNINGSOMRÅDE I KRONOBERGS LÄN* [online]. Länsstyrelsen i Kronobergs län.

Smits, A. J. M., Schmitz, G. H. W. & Van der Velde, G. (1992). Calcium-Dependent Lamina Production of Nymphoides peltata (Gmel.) O. Kuntze (Menyanthaceae): Implications for Distribution. *Journal of experimental botany* [online], 43(252). Available from: https://www.researchgate.net/publication/31435220_Calcium-Dependent_Lamina_Production_of_Nymphoides_peltata_Gmel_O_Kuntze_Menyanthaceae_Implications_for_Distribution. [Accessed 2024-11-12].

Stenmark, M., Segerlind, D. & Sandsten, H. (2020). *Inventering Sjögull i västra Mälaren 2019* [online].

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.

van der Voo, E. E. & Westhoff, V. (1961). *An Autecological Study of some Limnophytes and Helophytes in the area of the Large Rivers* [online]. State Institute for Nature Conservation Research, Bilthoven, The Netherlands.

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

7 Appendix 1: Rasters of explanatory variables