

Human impact footprint as a predictor of invasive species risk

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SLU, Vatten och miljö: Rapport 2025:15

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Publication: Digital only
Publication year: 2025

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Summary (Swedish and English)

Artutbredningsmodellering är ett värdefullt verktyg för att identifiera vilka områden som löper störst risk för spridning av potentiellt skadliga invasiva arter. Den bygger dock oftast på att man identifierar viktiga miljövariabler som påverkar arters spridning, till exempel (för akvatiska arter) vattenkemi, och sådana data kan vara ofullständiga i vissa intressanta områden eftersom de är resurskrävande att ta fram. Mänsklig aktivitet är känd som en viktig riskfaktor för att invasiva arter ska etablera sig och spridas, tillsammans med andra miljövariabler som vattenkemi, temperatur med mera. Här undersöker vi om ett enkelt index över mänsklig påverkan (eller “footprint”) kan användas som en förklarande variabel för att framgångsrikt förutsäga förekomsten av några viktiga invasiva akvatiska arter i svenska sjöar. Human footprint (HFP) fungerar bra först när det kombineras med medelårstemperatur (en viktig begränsande faktor för de flesta invasiva arter i Sverige), vilket ger resultat nära dem man får med en uppsättning relevanta miljövariabler, och kan vara användbart för att identifiera de sjöar som löper störst risk för spridning av invasiva arter. Där mer detaljerade miljövariabler också finns tillgängliga kan HFP bidra med ytterligare viktig information för modelleringen.

Species distribution modelling is a valuable tool for identifying areas most at risk of the spread of potentially harmful species. However, it usually relies on identifying key environmental variables that affect species spread such as (for aquatic species) water chemistry, and these data may not be comprehensive in some areas of interest as they are resource intensive to produce. Human activity is known to be an important risk factor for invasive species establishment and spread, alongside other environmental variables such as water chemistry, temperature etc. Here we examine whether a simple index of human impact levels (or “footprint”) can be used as an explanatory variable to successfully predict the presence of some important invasive aquatic species in Swedish lakes. Human footprint (HFP) performs well only when combined with mean annual temperature (an important limiting factor for most invasive species in Sweden), giving results close to those achieved with a set of relevant environmental variables and may be useful to identify lakes at most risk of the spread of invasive species. Where detailed environmental variables are also available, HFP can provide additional important information for modelling.

1 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 freshwater invasives are among the many species that have already responded to recent climate change by expanding their ranges in Europe (Alahuhta *et al.*, 2011). Freshwater ecosystems harbour disproportionately high biodiversity but face increasing threats from anthropogenic stressors, with invasive species recognised as an important driver of biodiversity loss (Dudgeon *et al.*, 2006; Reid *et al.*, 2019). Aquatic invasive species can fundamentally alter community structure and ecosystem function through predation, competition, disease transmission, and hybridisation, often producing irreversible impacts on native organisms (Havel *et al.*, 2015). Predicting the potential spread of invasive species is critical for informing management strategies, including early detection and rapid response measures. A key tool in combatting the establishment and spread of species that may be harmful in new areas is species distribution modelling, correlating known occurrence records with environmental variables to map habitat suitability and forecast range expansion under current and future conditions (Srivastava *et al.*, 2019). Detailed and granular environmental data such as water chemistry for individual lakes is ideal for this purpose, but this is not always available for all areas for obvious cost related reason. Human activity is known to be a key, and often the main, driver of invasive species spread (Leprieur *et al.*, 2008), and data can easily be obtained for any area based on remote sensing data and other freely available sources such as official statistics. Here we investigate how well an index of human impact level can function as a predictor in species distribution modelling.

Objectives of the study

- To explore how well human impact can predict the risk of invasive species occurrence in Swedish lakes.
- To compare a human impact only approach with more traditional environmental variables as predictors

1.1 Focal species

The species chosen were those included in HaVs “Fokuslista på främmande arter för miljöövervakare” which are also found in HaVs “Främmande arter i svenska vatten”. This resulted in the following species: *Cabomba caroliniana*, *Crassula helmsii*, *Ctenopharyngodon idella*, *Dreissena polymorpha*, *Elodea canadensis*, *Elodea nuttallii*, *Eriocheir sinensis*, *Hemigrapsus takanoi*, *Lepomis gibbosus*, *Neogobius melanostomus*, *Nymphoides peltata*, *Oncorhynchus gorbusha*, and *Pacifastacus leniusculus*. Some of these are species not found in lakes however, and when matched to lake polygons the species list was reduced to *Dreissena polymorpha*, *Elodea canadensis*, *Elodea nuttallii*, *Eriocheir sinensis*, *Nymphoides peltata*, *Pacifastacus leniusculus*. A further requirement for a minimum number of observations (10) in different lakes excluded *Dreissena polymorpha*.

1.2 Human impact

Human Footprint (HFP) data was sourced from (Gassert *et al.*, 2023) who employed and developed the methodology of (Sanderson *et al.*, 2002). This involved combining data on human pressures to map land cover types (built environments, crop lands and pasture lands).

They also mapped population density, and electric infrastructure, roadways, railways, and navigable waterways as a way of identifying both human impact and areas with easy access that are vulnerable even if not presently heavily impacted. Although the data are primarily terrestrial they can be considered as a proxy for propagule pressure in aquatic systems rather than a direct measure of habitat suitability. Each of these pressure layers received a score reflecting its level of human impact and was then standardised into a 0-50 scale by summing all the pressure layers. This resulted in a 100m resolution map displaying the combined index value HFP (see appendix for map of Sweden). Both the mean and maximum values were calculated from a 1km buffer around lakes and tested in modelling.

1.3 Environmental variables

The initial set of environmental variables was developed for use modelling invasive aquatic species in (Weldon & Meriggi, 2023), covering key physical, chemical, habitat and climate variables. See section 2.1 for details.

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 aquatic organisms 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) *Species occurrence data*

- Species included were the overlap of HaVs “Fokuslist på främmande arter för miljöövervakare” and HaVs list of “Främmande arter i svenska vatten”
- Artdatabanken, the Swedish Species Observation System: presence only records for the 2000-2025 period (<https://www.artportalen.se/>).
- The geographical coordinates of occurrence records were matched with the lakes polygon layer.
- A species was considered to be present in a lake when the number of occurrence records were ≥ 1 . 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).

- A lake polygon was classified depending on whether one of the observed species was present, this was a binary classification regardless of how many target species were found.

3) *Human Footprint Index*

- Level of human impact standardised into a 0-50 scale.
- Mean level calculated for 1km buffer around lakes
- Maximum level calculated for 1km buffer around lakes

4) *Environmental data/ explanatory variables*

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
- Area of lake
- 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. 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).
- Alkalinity. Spatial interpolation of measured alkalinity 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
- Wetlands. The proportion of wetland habitat within each catchment, taken from CORINE land cover at a resolution of 250 x 250 m
- Peat. The proportion of peatland habitat within each catchment, taken from CORINE land cover at a resolution of 250 x 250 m

Climate:

- Mean annual temperature for the location (SMHI)

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 version 4.2-6-2 (Guéguen et al., 2025). 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.

Presence records for invasive species were obtained from the Swedish Species Observation System (Artportalen), retaining only validated observations. Presence records were spatially matched to lake polygons using a 100 m buffer to account for coordinate uncertainty. Species with fewer than 10 presence records were excluded from modeling. A target-group background approach for pseudo-absence generation was used. Background locations were restricted to lakes where sampling effort had been documented through observations of any fish species or the widespread aquatic plant *Nuphar lutea*. This approach controls for spatial sampling bias inherent in citizen science data. For each species, 1,000 pseudo-absences were randomly selected from this target-group background, replicated across 10 pseudo-absence sets to account for stochasticity in background selection. To generate a composite measure of invasion risk, we stacked individual species predictions for each scenario.

Of the target species included, *Eriocheir sinensis* had a low number of lake matches (10) which could potentially give unstable estimates of TSS/ROC. The analysis was repeated excluding this species as a sensitivity check, without any significant changes to results.

For each lake, we calculated the maximum predicted probability across all modelled species, representing the probability of occurrence of the most likely invasive species. This approach addresses the question of whether human footprint predicts the presence of *any* invasive species rather than focussing on modelling each species independently. The choice of maximum rather than mean reflects the key concern here being to investigate how well HFP predicts the risk of invasive species as a general category rather than any particular species.

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 and evaluated using 3-fold cross-validation.

The following interpretation of 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 individual models

As expected, the AUC ROC and TSS scores are variable, depending on the modelling method used and the explanatory variables included (Fig. 1). In the scenarios (i.e. different sets of explanatory variables), the combination of maximum HFP and mean annual temperature performed best, although results are very close to those for natural variables and the maximum HFP, and natural variables only. HFP Max alone clearly performed better than HFP mean, with HFP mean being the weakest set of models.

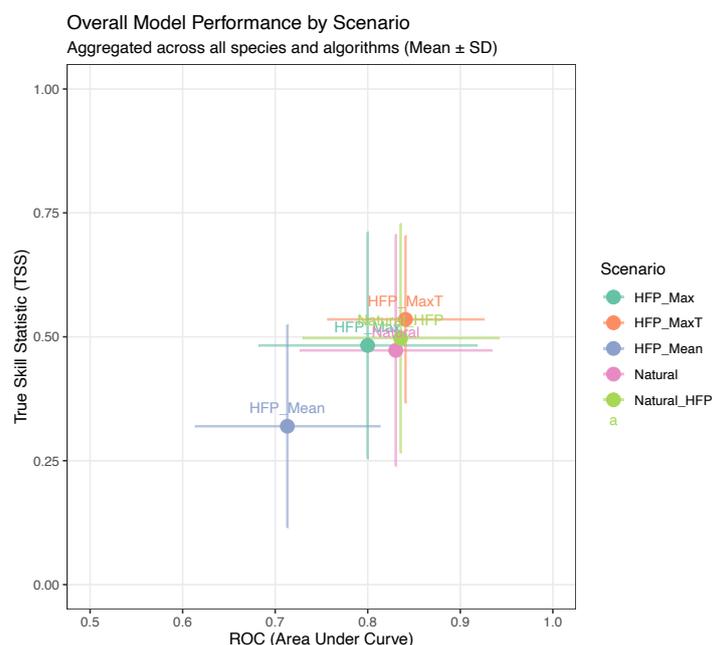


Figure 1: TSS and ROC values for all statistical methods use in the scenarios. HFP is human footprint (maximum or mean value), Natural is the set of environmental explanatory variables, while HFP_MaxT is maximum HFP plus mean annual temperature.

3.1.2 Validation of ensemble models by scenario

When the multiple models shown in Fig. 1 are combined to an ensemble model, individual model contributions are performance weighted and models with very weak predictive performance are excluded entirely ($TSS < 0.3$). The resulting ensemble models (Fig. 2) show that the natural variables and natural variables in combination with maximum HFP had the best performance. Maximum HFP and mean temperature is next best, followed by maximum HFP, with mean HFP in clear last place. All ensemble models however showed a performance that could be characterised as fair or good.

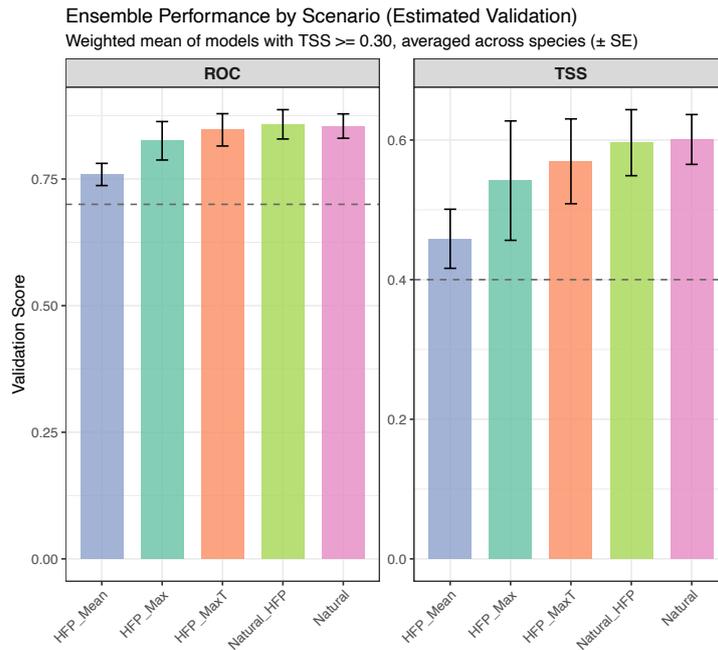


Figure 2: Validation scores (ROC and TSS) for the scenarios modelled

3.1.3 Projections based on models

The modelled projection of probability of occurrence across all lakes is shown in Fig. 3. All lake polygons are coloured according to the probability of occurrence of at least one of the focus species. The two human footprint only projections show higher probabilities for many northerly locations, particularly along the coast. The natural variables in contrast show the highest probabilities in a band roughly encompassing lakes Mälaren, Vänern and Vättern with a second hotspot in Skåne, and generally higher probabilities close to the coast in the southern third of Sweden. This latter distribution is largely reflected in the projection based on human footprint with the addition of temperature. Again the three large lakes are the focus of a band of high risk and Skåne is highlighted, the main difference being this model assigns somewhat lower probabilities in the north of Sweden.

The models based on natural variables rank mean annual temperature, lake depth, alkalinity and lake connectivity as the most important explanatory factors, and when human impact is

included it is ranked as either the most important or second behind temperature, depending on the model (Fig. 4)

Top 100 highest-risk lakes across scenarios
 Blue points = top 100 | Background = all lakes (max prob)

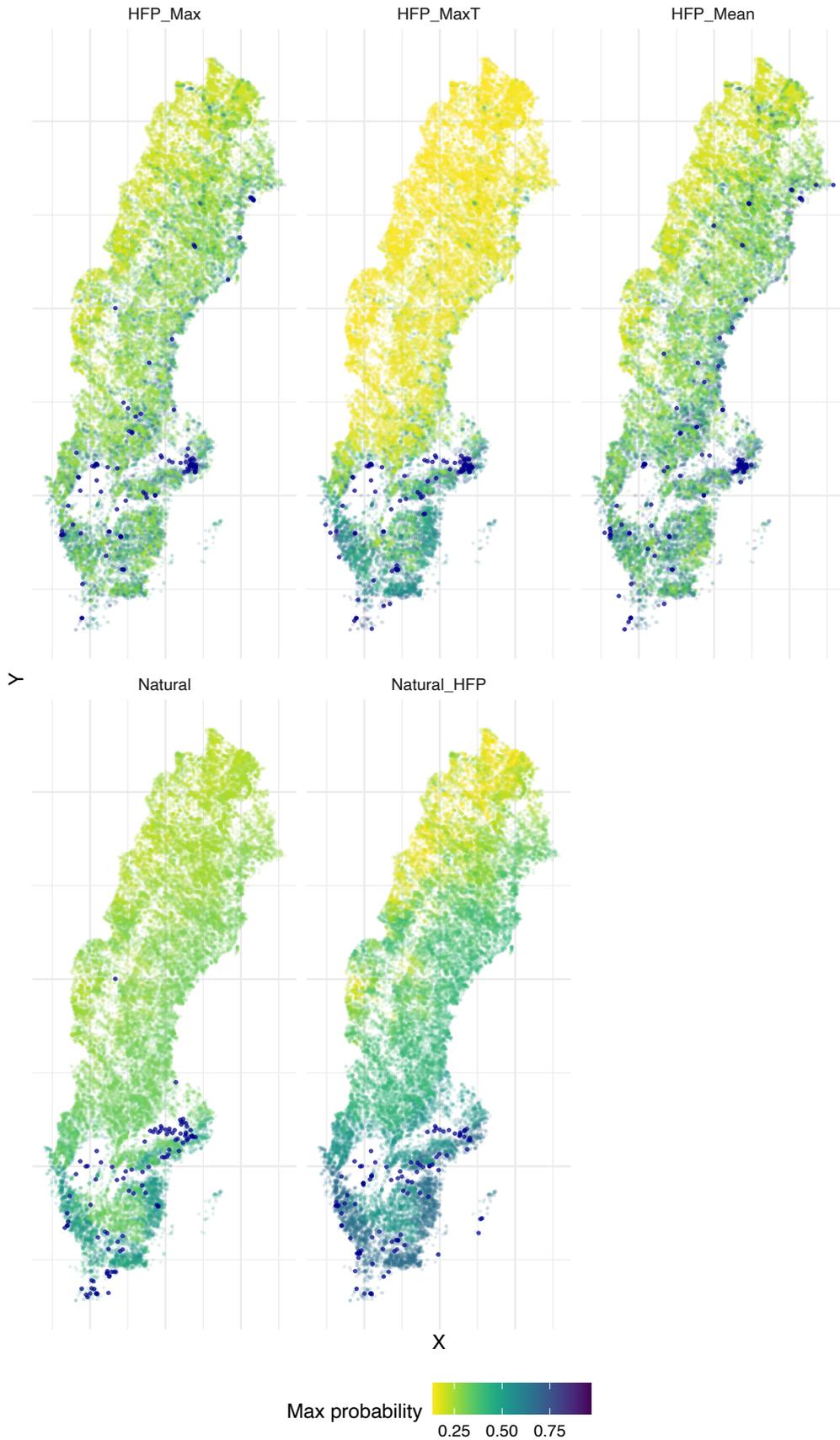


Figure 3: Modelled probability of invasive species in Swedish lakes and the 100 lake polygons with highest probability of occurrence as points. . HFP is human footprint (maximum or mean value), Natural is the set of environmental explanatory variables, while HFP_MaxT is maximum HFP plus mean annual temperature.

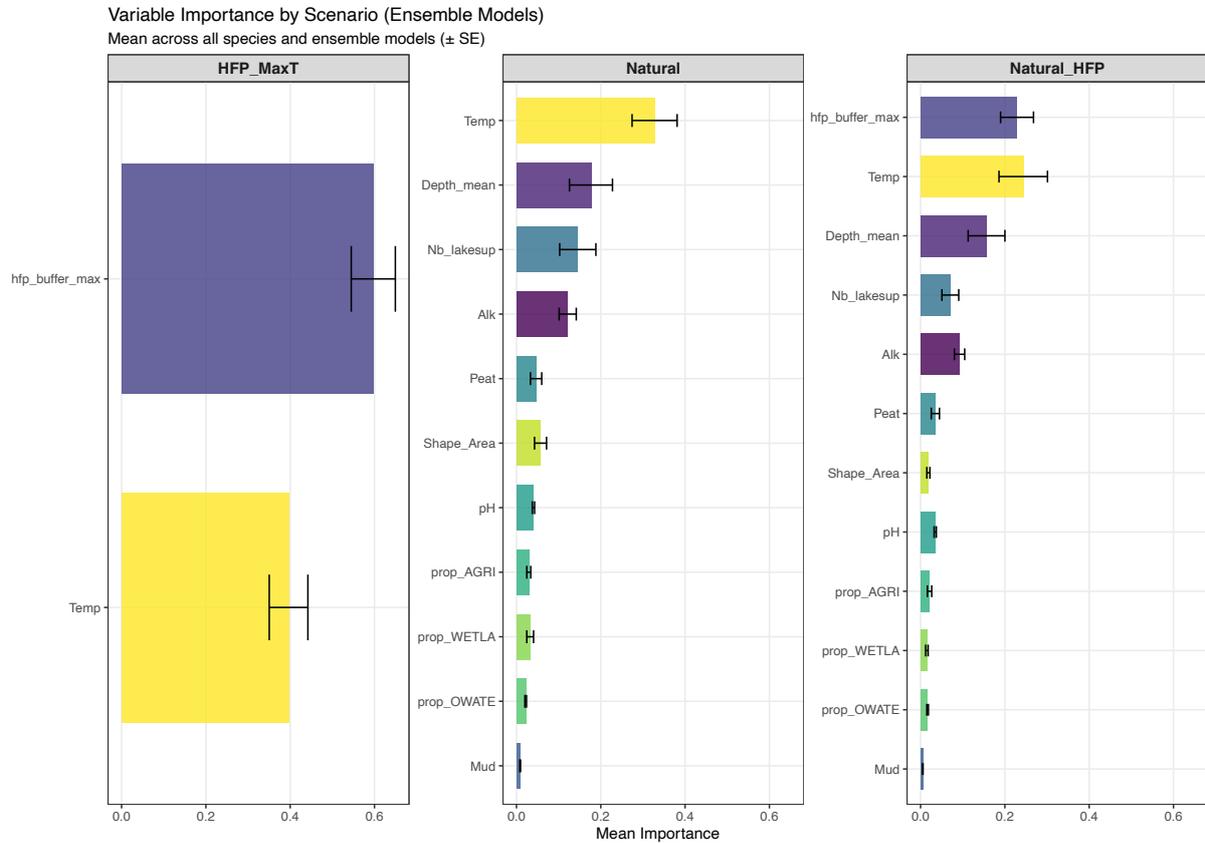


Figure 4: Variable importance by scenario (only for scenarios where more than one explanatory variable were included)

4 Discussion and conclusion

The human footprint index (HFP) when used alone performs moderately well, although the maximum value is notably better than the mean, indicating that small areas of more intense human activity may be more important to the spread of invasive species than a more widespread but lower intensity impact (a speculative example could be that the presence of a main road near a lake may indicate many more people coming to visit that lake than the equivalent m² of small country roads spread over the same surrounding area would). However, a clear failing of the HFP only models in a Swedish context is that temperature is often a limiting factor for the spread of invasive species, and this is not taken into account in a pure HFP approach. As a result, the HFP models indicate far more risk areas in northern Sweden while the natural variables suggest a lower probability north of the Mälaren to Vänern band (Fig. 3). Adding mean annual temperature to maximum HFP produces a map more like that of the natural variables model with the highest risk lakes in a very similar distribution. In other words, HFP-

only modelling exaggerates the risks in northern, lower temperature lakes. This suggests that as long as the key limiting factor of temperature is also included, HFP can be useful as a way of identifying risk areas, especially where more detailed environmental data such as specific lake water chemistry is not available. Of course, such a generalist approach is unlikely to be the best modelling method if a particular invasive species is in focus. In this case the usual process of identifying key explanatory variables that are limiting for that species will almost certainly give better results. For example where a certain pH level constitutes an obstacle, or where there is a requirement for a minimal level of calcium for a species to establish and reproduce then including that information in models where possible is always the preferred approach. Where such detailed information is lacking though, or as a first pass to establish which lakes might be at higher risk from any invasive species the application of an index of human impact levels such as HFP is clearly a useful tool. Even where more detailed environmental variables such as water chemistry are available, a measure of human impact is likely to improve models as an additional explanatory factor, as shown by the strong performance here of natural variables in combination with maximum HFP (Fig. 2).

5 Acknowledgements

Thanks are due 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>.
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J. & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews of the Cambridge Philosophical Society* [online], 81(02), p. 163 Wiley. Available from: <http://dx.doi.org/10.1017/S1464793105006950>. [Accessed 2025-12-12].
- Friedman, J. H. (1991). *Estimating functions of mixed ordinal and categorical variables using adaptive splines* [online]. Stanford Univ CA Lab for Computational Statistics.
- Gassert, F., Venter, O., Watson, J. E. M., Brumby, S. P., Mazzariello, J. C., Atkinson, S. C. & Hyde, S. (2023). An operational approach to near real time global high resolution mapping of the terrestrial Human Footprint. *Frontiers in Remote Sensing* [online], 4(1130896), p. 1130896 Frontiers Media SA. Available from: <http://dx.doi.org/10.3389/frsen.2023.1130896>. [Accessed 2025-12-12].
- Guéguen M, Blancheteau H, Lemaire-Patin R, Thuiller W (2025). *biomod2: Ensemble Platform for Species Distribution Modeling*. R package version 4.2, <https://biomodhub.github.io/biomod2/>.
- 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>.
- Havel, J. E., Kovalenko, K. E., Thomaz, S. M., Amalfitano, S. & Kats, L. B. (2015). Aquatic invasive species: challenges for the future. *Hydrobiologia* [online], 750(1), pp. 147–170 Springer Science and Business Media LLC. Available from: <http://dx.doi.org/10.1007/s10750-014-2166-0>. [Accessed 2025-12-12].
- Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T. & Brosse, S. (2008). Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS biology* [online], 6(2), p. e28 Public Library of Science (PLoS). Available from: <http://dx.doi.org/10.1371/journal.pbio.0060028>. [Accessed 2025-12-12].
- 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].

- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D. & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity: Emerging threats to freshwater biodiversity. *Biological reviews of the Cambridge Philosophical Society* [online], 94(3), pp. 849–873 Wiley. Available from: <http://dx.doi.org/10.1111/brv.12480>. [Accessed 2025-12-12].
- Ridgeway, G. *The state of boosting*. [online] (1999). Available from: [http://www.planchet.net/EXT/ISFA/1226.nsf/0/a29acbd26d902d6fc125822a0031c09b/\\$FILE/boosting.pdf](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>.
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V. & Woolmer, G. (2002). The human footprint and the last of the wild. *Bioscience* [online], 52(10), p. 891 Oxford University Press (OUP). Available from: [https://dx.doi.org/10.1641/0006-3568\(2002\)052\[0891:THFATL\]2.0.CO;2](https://dx.doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2). [Accessed 2025-12-12].
- 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>.
- Srivastava, V., Lafond, V. & Griess, V. C. (2019). Species distribution models (SDM): applications, benefits and challenges in invasive species management. *CAB Reviews Perspectives in Agriculture Veterinary Science Nutrition and Natural Resources* [online], 2019(020), pp. 1–13 CABI Publishing. Available from: <http://dx.doi.org/10.1079/pavsnr201914020>.
- 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>.
- Weldon, J. & Meriggi, C. (2023). Modelling the risks of invasive aquatic species spread in Swedish lakes. *Rapport / Sveriges lantbruksuniversitet, Institutionen för vatten och miljö* [online], (2023:1). Available from: <https://res.slu.se/id/publ/120801>. [Accessed 2023-03-23].
- 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: Raster of human footprint index values

