

Modelling temperature-driven changes in species associations across freshwater communities

Sam Wenaas Perrin¹  | Bert van der Veen^{2,3}  | Nick Golding^{4,5,6}  | Anders Gravbrøt Finstad¹ 

¹Centre of Biodiversity Dynamics, Department of Natural History, Norwegian University of Science and Technology, Trondheim, Norway

²Department of Landscape and Biodiversity, Norwegian Institute of Bioeconomy Research, Trondheim, Norway

³Department of Mathematical Sciences, Norwegian University of Science and Technology, Trondheim, Norway

⁴Telethon Kids Institute, Perth Children's Hospital, Nedlands, Western Australia, Australia

⁵Curtin University, Bentley, Western Australia, Australia

⁶Department of BioSciences, University of Melbourne, Parkville, Victoria, Australia

Correspondence

Sam W. Perrin, Centre of Biodiversity Dynamics, Department of Natural History, Norwegian University of Science and Technology, N-7491 Trondheim, Norway. Email: sam.perrin@ntnu.no

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Abstract

Due to global climate change-induced shifts in species distributions, estimating changes in community composition through the use of Species Distribution Models has become a key management tool. Being able to determine how species associations change along environmental gradients is likely to be pivotal in exploring the magnitude of future changes in species' distributions. This is particularly important in connectivity-limited ecosystems, such as freshwater ecosystems, where increased human translocation is creating species associations over previously unseen environmental gradients. Here, we use a large-scale presence-absence dataset of freshwater fish from lakes across the Fennoscandian region in a Joint Species Distribution Model, to measure the effect of temperature on species associations. We identified a trend of negative associations between species tolerant of cold waters and those tolerant of warmer waters, as well as positive associations between several more warm-tolerant species, with these associations often shifting depending on local temperatures. Our results confirm that freshwater ecosystems can expect to see a large-scale shift towards communities dominated by more warm-tolerant species. While there remains much work to be done to predict exactly where and when local extinctions may take place, the model implemented provides a starting-point for the exploration of climate-driven community trends. This approach is especially informative in regards to determining which species associations are most central in shaping future community composition, and which areas are most vulnerable to local extinctions.

KEYWORDS

climate change, co-occurrence, fish, JSDMs

1 | INTRODUCTION

Due to global trends in species distribution range shifts and biodiversity loss, ecosystems worldwide are likely to undergo considerable changes in community composition (Jennings & Harris, 2017;

Seebens et al., 2020). Along with the increased spread of non-native species as a result of globalisation, increasing average temperatures due to climate change will enable new species to make their way into environments previously too cold for them to either enter or establish in (Rahel & Olden, 2008; Sharma et al., 2007;

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Walther et al., 2005). Many of these species are capable of causing extirpations of native species or even the restructuring of entire food webs once established (Nackley et al., 2017; Rockwell-Postel et al., 2020; Walther et al., 2009). Many species are vulnerable to local population declines and extinctions as increasing temperatures and extreme weather events compound threats posed by other anthropogenic factors, among them biological invasions (Dawson et al., 2011).

A changing climate is also capable of changing associations between species. While many species may be capable of co-occurring at certain temperatures, as annual temperatures increase, one species may gain a competitive advantage. For instance, at moderate temperatures a beech forest may contain three or four species, yet as temperatures tend to either extreme, negative associations may occur in the form of a single species beginning to outcompete the others and dominate (Leathwick, 2002). Associations becoming more negative with temperature increases could lead to declines in some species' populations, and local extinctions occurring, well before these species' upper thermal tolerances are reached. A deeper understanding of changes in species associations over a temperature gradient would contribute greatly to our understanding of the likely effects of climate change on community composition (Early & Keith, 2019; Freeman et al., 2018).

Climate change is likely to affect freshwater ecosystems particularly harshly, with a rise in temperature likely to lead to a population increase in species with higher thermal tolerance, with species of lower tolerance shifting further upstream (Comte et al., 2013; Daufresne & Boët, 2007). Increases in human translocations over recent decades are leading to novel species associations (Carpio et al., 2019), making understanding the impacts of these associations particularly important to predict future ecosystem effects. Research in sub-Arctic regions – which are likely to warm substantially in the coming decades – has already demonstrated a shift towards more warm-adapted species both within individual lakes and across catchments. (Hayden et al., 2017; Sharma et al., 2007; Van Zuiden et al., 2015; Winfield et al., 2008). Northern pike (*Esox Lucius*; Linnaeus, 1758) and brown trout (*Salmo trutta*; Linnaeus, 1758) may co-occur at lower temperatures in the sub-Arctic, but as average annual temperatures increase, a negative association

results in a drop in the brown trout population as pike begin to predate brown trout at higher rates, eventually leading to local brown trout extinctions (Hein et al., 2013). The accelerated nature of climate change in the Arctic and sub-Arctic means that these regions are particularly important in giving an insight into potential community shifts, which are likely to take place in the coming decades in warmer regions.

Although much of the current research on shifts in associations over a temperature range concerns only a few species, or at a relatively small scale, attempts to increase focus on broader community models in predicting the impacts of climate change at a larger scale are ongoing (Comte et al., 2013; Radinger et al., 2019; Silknetter et al., 2020). Here, we construct a Joint Species Distribution Model (JSDM) as proposed by Tikhonov et al. (2017) to predict trends in species associations across a temperature gradient on a multi-national scale. JSDMs arose as a combination of habitat modelling and community ecology, in response to the need to account for associations which are not explained by the effects of environmental covariates (Ovaskainen et al., 2017; Pollock et al., 2014; Warton et al., 2015). Although they are capable of estimating correlations between species, these correlations may be a product of shared habitat specialisation, not interactions (Hargreaves et al., 2020; Hayden et al., 2013). As such, the output of JSDMs are often referred to as representing species associations, as opposed to interactions (Blanchet et al., 2020).

Here we use a dataset containing presence-absence data of fish species across more than 3000 freshwater lakes in the region of Fennoscandia, covering large climate gradients across mainland Norway, Sweden and Finland (Tammi et al., 2003). Using this modelling framework we aim to assess (a) whether we are able to identify the changes in associations between species of different thermal tolerances over a temperature gradient at large scales, (b) the reliability of our predictions based on whether these associations corroborate the results of previous research into pairwise associations and (c) how accurately these models can be used to predict future community shifts in the face of climate change. We aim to provide ecological modellers with a promising framework to build upon when exploring shifts in species distributions and abundances and provide managers with key information regarding potential extinction and invasion hotspots going forward.

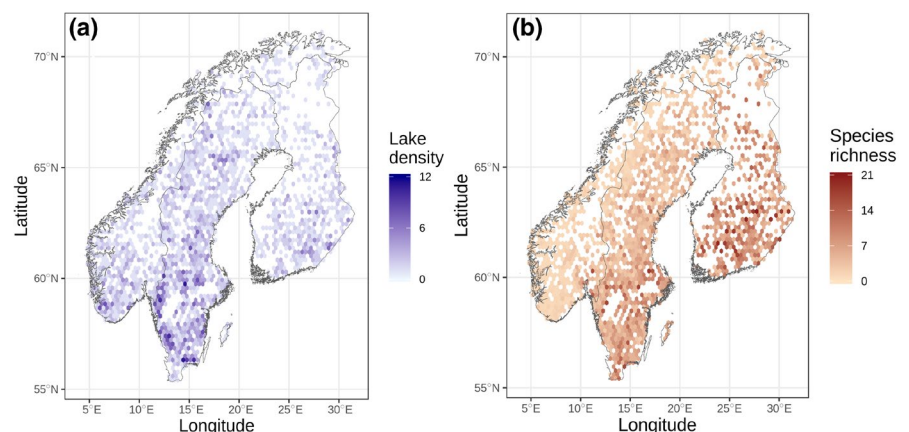


FIGURE 1 (a) Density of the 3308 lakes surveyed in the 1995 Nordic Fish Status Survey, represented by the number of lake centrepoints contained within hexagons. (b) Distribution of freshwater fish species richness across the same lakes, with species richness equal to average species richness of lakes found within hexagons

2 | METHODS

2.1 | Study system

Our study system was a series of 3308 lakes throughout the Fennoscandian region (Norway, Sweden and Finland). The lakes were located between 55.4 degrees and 71.1 degrees in latitude, 4.6 and 31.4 degrees longitude (WGS84), and at an altitudinal range of 0 to 1540 m. Surveyed lake density is highest throughout Sweden (Figure 1a).

The region itself is particularly species poor, given relatively recent deglaciation (Huitfeldt-Kaas, 1918). Species richness increases eastwards, with Finland and Sweden showing higher species richness than western Norway (Figure 1b). This is a product of mountainous regions dividing Norway, which have provided fewer immigration pathways for freshwater fish. Studies in the region have predicted that native species belonging to warmer guilds ('cool-water species'), like the Northern pike, the European perch (*Perca fluviatilis*; Linnaeus, 1758), and cyprinids like the common roach (*Rutilus rutilus*; Linnaeus, 1758) (Elliott, 2010; Hayden et al., 2014; Hokanson, 1977; Wehrly et al., 2003) will expand their range (Comte et al., 2013; Hayden et al., 2017). This could result in the local extirpation of species like the brown trout, whitefish (*Coregonus lavaretus*; Valenciennes, 1848) and Arctic charr (*Salvelinus alpinus*; Linnaeus, 1758), which are more tolerant of cold waters ('cool-cold/cold-water species'; Elliott, 2010; Hayden et al., 2014; Parkinson et al., 2016; Wehrly et al., 2003). The co-occurrence of species from various thermal guilds, within Fennoscandia, makes the region ideal for studying the impacts of climate change on freshwater communities (Comte et al., 2013).

2.2 | Occurrence data

The occurrence data were collected from a Fennoscandian survey of freshwater fish, originally conducted between 1995 and 1997 (Tammi et al., 2003). The resulting dataset consists of presence-absence information on fish species in 3821 lakes across Fennoscandia (Table 1). Henceforth, all species will be referred to by their common name (Table 1). Species that appeared in less than 1% of total lakes were excluded, as it is unlikely species-specific parameters can be accurately estimated given such low levels of occurrence. None were species thought likely to have a large-scale negative impact on Fennoscandian freshwater communities, either through competition or direct predation (for the full list of species, see Appendix S1).

2.3 | Environmental data

Temperature data were derived from the EuroLST data set for the centre of each lake (Metz et al., 2014). The temperature covariate used was the average air temperature of the warmest quarter, which has shown to have a strong correlation with water lake temperature

(Livingstone & Lotter, 1998). This was the available data most likely to be strongly correlated with ice-off dates and spring warming temperatures, both of which have been shown to have a strong effect on both the life histories of aquatic species and interactions between different species (Mehner et al., 2011; Munsch et al., 2019).

For each lake, we obtained six additional covariates describing either environmental properties or human impact with the potential to influence establishment risk. Our study focuses on the effect of temperature; however, other environmental covariates are likely to have a strong effect on community composition, and as such are included as covariates. Environmental properties included lake surface area, shoreline complexity, total area of lakes situated upstream of focal lake, water pH, total organic carbon and human impact at the site. Area, shoreline complexity, and total upstream area were all derived from GIS analyses. Shoreline complexity was then calculated as:

$$SC = \frac{P}{2000\sqrt{\pi A}},$$

where P is the lake perimeter and A is the lake surface area (Wetzel, 2001). Water chemistry covariates were taken from the 1995 Nordic Lake Survey (Henriksen et al., 1998). To approximate human impact on each site, we used the Human Footprint Index as compiled by Venter et al. (2016), henceforth referred to as HFI. HFI is a point score which combines eight human impact covariates to approximate the level of human pressure on nature, assigned to cells one kilometre squared in size (Venter et al., 2016). These impact covariates include presence of built environment, crop lands and roads, and local human population density. HFI was taken for the cell in which the centre point of the lake lay, with previous research suggesting that human activity in the immediate vicinity of freshwater sites is more likely to affect species occurrences than activity upstream or downstream (Chapman et al., 2019). Lakes for which any of the environmental data was incomplete were disregarded ($n = 119$, 3.5% of total lakes). Area, total upstream area and total organic carbon were heavily right skewed and were thus log-transformed to assist with model convergence. All covariates were standardised by scaling to a mean of zero and a standard deviation of one to assist in model convergence. Further information on all covariates, included expected effects on populations, are summarised in Table 2.

The immigration history of freshwater fish in the area and steep topography that makes up much of Norway's west coast mean that many species have historically been unable to naturally colonise this region (Figure 1b; Huitfeldt-Kaas, 1918; Sandlund & Hesthagen, 2011). As such, environmental conditions which would normally result in the presence of species across other parts of Fennoscandia may have little to no effect on the likelihood of their presence in this region. This spatial divide could potentially make for a source of spatial autocorrelation, so to account for this we used the historical distribution range of species which were unable to colonise Norway's west coast as an additional covariate (see Appendix S2).

TABLE 1 Freshwater fish species surveyed in the 1995 Nordic Fish Status Survey

Common name	Scientific name	Family	Naming authority	Frequency of occurrence (%)
Perch	<i>Perca fluviatilis</i>	Percidae	Linnaeus, 1754	72.1
Pike	<i>Esox lucius</i>	Esocidae	Linnaeus, 1754	65.8
Roach	<i>Rutilus rutilus</i>	Cyprinidae	Linnaeus, 1754	52.9
Brown trout	<i>Salmo trutta</i>	Salmonidae	Linnaeus, 1754	46.7
Burbot	<i>Lota lota</i>	Lotidae	Linnaeus, 1754	37.8
Bream	<i>Abramis brama</i>	Cyprinidae	Linnaeus, 1754	24.5
Whitefish	<i>Coregonus lavaretus</i>	Salmonidae	Valenciennes, 1844	23.5
Ruffe	<i>Gymnocephalus cernuus</i>	Percidae	Linnaeus, 1754	21.0
Arctic charr	<i>Salvelinus alpinus</i>	Salmonidae	Linnaeus, 1754	14.9
Bleak	<i>Alburnus alburnus</i>	Cyprinidae	Linnaeus, 1754	13.7
Tench	<i>Tinca tinca</i>	Cyprinidae	Linnaeus, 1754	13.5
Vendace	<i>Coregonus albula</i>	Salmonidae	Linnaeus, 1754	12.1
Zander	<i>Stizostedion lucioperca</i>	Percidae	Linnaeus, 1754	11.7
Crucian carp	<i>Carassius carassius</i>	Cyprinidae	Linnaeus, 1754	11.0
Rudd	<i>Scardinius erythrophthalmus</i>	Cyprinidae	Linnaeus, 1754	10.1
Minnow	<i>Phoxinus phoxinus</i>	Cyprinidae	Linnaeus, 1754	9.2
Smelt	<i>Osmerus eperlanus</i>	Osmeridae	Linnaeus, 1754	8.1
White bream	<i>Blicca bjoerkna</i>	Cyprinidae	Linnaeus, 1754	6.5
Grayling	<i>Thymallus thymallus</i>	Salmonidae	Linnaeus, 1754	6.1
Ide	<i>Leuciscus idus</i>	Cyprinidae	Linnaeus, 1754	6.0
Rainbow trout	<i>Oncorhynchus mykiss</i>	Salmonidae	Walbaum, 1792	4.1
Threespine stickleback	<i>Gasterosteus aculeatus</i>	Gasterosteidae	Linnaeus, 1754	1.6
Brook trout	<i>Salvelinus fontinalis</i>	Salmonidae	Mitchill, 1814	1.4
Ninespine stickleback	<i>Pungitius pungitius</i>	Gasterosteidae	Linnaeus, 1754	1.0

Note: Table shows species taxonomy, as well as percentage of 3308 lakes that the species were found in. Species in bold occurred in more than 10% of lakes and were, thus, considered high-occurrence species.

2.4 | Statistical modelling

We constructed a JSDM which predicts changes in species associations over a temperature gradient. For our matrix of recorded observations, we assume that the presence-absences of species $j = 1 \dots p$ at lakes $i = 1 \dots n$ are independent observations, conditional on a vector of $h = 1 \dots n_f$ latent factors per lake, modelled as:

$$y_{ij} \sim \text{Bernoulli}(p_{ij}),$$

$$\text{with } p_{ij} = \varphi^{-1}(\eta_{ij}),$$

where p_{ij} denotes the probability of species j being present at site i , and φ^{-1} denotes the inverse of a probit link-function. We denote η_{ij} as:

$$\eta_{ij} = \alpha_j + \sum_{k=1}^{n_c} x_{ik} \beta_{jk} + \varepsilon_{ij},$$

where x_{ik} denotes the value of environmental covariate $k = 1 \dots n_c$ at site i , α_j denotes the intercept for species j , and β_{jk} denotes the effect

of environmental covariate k on species j . The species-by-site random effects $\varepsilon_{ij} \sim N(0, R(x_i))$ are defined by a latent factor model:

$$\varepsilon_{ij} = \sum_{h=1}^{n_f} z_{ih} \lambda_{jh}(x_i^*),$$

where z_{ih} denotes our $h = 1 \dots n_f$ latent factors for lake i , where $\lambda_{jh}(x_i^*)$ denotes the responses (loading) of species $j = 1 \dots p$ to each of the latent factors. We model the loadings per species j and for each factor h as a function of temperature:

$$\lambda_{jh}(x_i^*) = \sum_{i=1}^{n_i} \tau_{jh} + x_i u_{jh},$$

where τ_{jh} denotes an additional intercept for species j and latent factor h , u_{jh} denotes the response of latent factor h for species j to temperature, x_i denotes the temperature in degrees at site i , and n_i denotes the total number of sites. Here, we assume $n_f = 3$, as our Deviance information criteria did not improve significantly with the addition of more latent factors, and a few major gradients usually account for

TABLE 2 Environmental covariates, description, environmental effects, units and mean (\pm standard deviation) used in Joint Species Distribution Models of freshwater fish across European freshwater lakes

Environmental covariate	Description	Expected biological effect	Unit	Mean (\pm SD)
Area	Surface area of lake	Larger area increases potential habitat and niche breadth	Square kilometres	6163 (\pm 52149)
Shoreline complexity	Calculated using area and perimeter	Increased shoreline complexity creates variation in habitat type (Verdiell-Cubedo et al., 2012)	Unitless	0.20, 0.14
Temperature	Average surface air temperature during maximum quarter	Temperature may alter various life history aspects of species (Magnuson et al., 1979)	Degrees	12.75, 1.74
Human Footprint Index	Index comprising 10 different variables, which represents impact of human activity (Venter et al., 2016)	Higher HFI increases chances of local human introductions (Chapman et al., 2019)	Unitless scale from 1 to 50	6.79, 7.03
Total upstream area	Aggregated area of lakes occurring directly upstream from focal lake	Higher upstream area increases chance of species' persistence	Square kilometres	388.68, 6405.17
pH	Taken from Nordic Lake Survey (Henriksen et al., 1998)	Acid sensitivity can limit local species' distributions (Ohman et al., 2006)	Unitless scale from 1 to 14	6.62, 0.66
Total organic carbon	Taken from Nordic Lake Survey (Henriksen et al., 1998)	Higher levels can cause anoxia and limit species' distributions (Ohman et al., 2006)	Mg per litre	7.09, 4.95
Biogeographic zone	Whether or not lake was found in a drainage basin cut-off from the rest of the region by the natural dispersal barrier running through central Norway	Presence of dispersal barrier provides fewer immigration pathways into western Norway for species, which did not colonise area via Norwegian Sea (Sandlund & Hesthagen, 2011)	Binary covariate	NA

most inter-species variation (Halvorsen, 2012). We define the matrices $\Lambda(x_i^*)$ with elements $\lambda_{jh}(x_i^*)$ and use these to construct a temperature-dependent, inter-species residual covariance matrix:

$$\Omega(x_i^*) = \Lambda(x_i^*) \Lambda(x_i^*)^T + I.$$

We then scale this covariance matrix to an inter-species correlation matrix R representing temperature-dependent associations between species that are not explained by fixed species-specific effects of environmental covariates:

$$R_{j_1j_2} = \Omega_{j_1j_2} / \sqrt{\Omega_{j_1j_1} \Omega_{j_2j_2}}.$$

These resulted in values between -1 and 1 , with positive values indicative of positive associations between species, implying that species are likely to co-occur, and negative values implying the opposite. To compare species associations to the similarity in species

responses to fixed effects in the models, we calculated an additional correlation matrix (Hui, 2017).

Although temperature was included in the random-effect, it was also included as a fixed-effect with quadratic function, to account for potential non-linear responses of species to temperature (Boddy & McIntosh, 2017; Veen et al., 2021).

We fit the model in a Bayesian framework using the greta R-package (Golding, 2019). All parameters were specified non-informative normally-distributed priors with a mean of zero and a standard deviation of 10, with the exception of the latent factors z_{jh} (mean = 0, SD = 1) and alpha parameters α_j (mean = -2 , SD = 1). Alpha parameters had a lower mean to assist with convergence, as most species were prevalent at a low number of locations. Further exceptions were u and τ matrices, for which the diagonals had positively truncated non-informative normal priors, and all values in the upper triangle, which were set to zero to enforce identifiability (Hui et al., 2015). Markov Chain Monte-Carlo (MCMC) sampling was done

using 4000 samples on one chain, with a burn-in of 2000 samples. Although most Bayesian analyses would use multiple chains, latent variable models are often invariant to sign-switching (Hui, 2017), so here we choose to only run one chain. We used a Hamiltonian Monte Carlo sampler, sampling the number of leapfrog steps at each iteration uniformly between 40 and 60 (these numbers were manually tuned to achieve efficient sampling). The leapfrog integrator step sizes for each parameter were automatically tuned during the burn-in phase, then fixed for sampling. Parameters were considered to have adequately converged if their Geweke Z-score was below 1.96 (Geweke, 1992). 96 of our 105 species association parameters converged adequately. Trace plots for all association parameters can be found in Appendix S3.

We estimated changes in species associations over a continuous gradient from 6.68 to 16.80 degrees Celsius, which represented the minimum and maximum temperature observed in the data. Three models were constructed. Model 1 included data from all 24 species ("all species" model). Model 2 included data from species which only occurred in more than 10% of lakes (henceforth referred to as high-occurrence species, which are indicated as bold names in Table 1), as we wanted to test whether the inclusion of low-occurrence or low-detectability species produced a better model fit for commonly occurring species. Of the 24 species included in this study, 15 were classified as high-occurrence, and were thus used in model 2 (the "reduced species" model). To test whether accounting for species associations over a temperature gradient improved model fit, model 3 accounted for species associations, but not over a temperature gradient ("base JSDM" model). In this model, ϵ_{ij} is defined as:

$$\epsilon_{ij} = \sum_{h=1}^{n_i} z_{ih} \lambda_{jh}$$

Model fit was quantified using the Bernoulli deviance D_j , where

$$D_j = -2 \times \sum_i (y_{ij} \log(\mu_{ij}) + (1 - y_{ij}) \log(1 - \mu_{ij})),$$

which was calculated for each high-occurrence species j of each model using the posterior medians of p_{ij} . To ensure that our models were an improvement over single species distribution models (SDMs), we created a stacked species distribution model (SSDM) consisting of single species distribution models for the fifteen species with occurrences in over 10% of lakes. These were also probit models with a Bernoulli distribution and used the same environmental covariates as our three previous models, but they did not include latent factors to account for associations between species. Model fit between the three models was compared using the improvement in deviance D_j from the SSDM for each of the high-occurrence species.

All statistical analyses were completed using R version 3.4.4 (R Core Team, 2017) and RStudio (RStudio Team, 2020). Additionally, the following R-packages were used for analysis and visualisation; dplyr (Wickham et al., 2019), rgeos (Bivand & Rundel, 2019), spdep (Bivand & Wong, 2018), postGIStools (Marchand & Ellison, 2019),

tensorflow (Allaire & Tang, 2019), corrplot (Wei & Simko, 2017), ggplot2 (Wickham, 2016), magrittr (Bache & Wickham, 2014) and gridExtra (Auguie, 2017). A comprehensive definition of the model, the code, and its analysis can be found at Perrin (2021) (<https://doi.org/10.5281/zenodo.4665778>).

3 | RESULTS

Our results captured variations in species associations across a temperature gradient, with many negative associations between cold-water species and those tolerant of warmer temperatures.

Model fit was relatively similar across the all species model, reduced species model and base JSDM for each species (Figure 2). The only notable exceptions were brown trout, tench and arctic charr, for which the reduced species model (model two) had better model fit than either one of or both the other models. As such, the reduced species model was used for further analysis, as computing time was considerably lower. Biogeographic zone did not have a significant effect on any species and did not affect species associations, and as such the covariate was removed from all models.

Although several species associations at lower temperatures were negative – indicating a low likelihood of co-occurrence – at the mean and higher temperatures most associations between species were positive or close to neutral (Figure 3). The majority of negative associations between species at mean or high temperatures occurred between the cold-water species (brown trout or Arctic charr) and other species, with the most negative associations occurring between these species and those classified as belonging to a higher thermal guild (roach, perch and pike). Correlations in response to aggregated environmental variables were positive between the majority of species, with the exception of Arctic charr, for which many correlations were negative (Figure 4a). Correlations between species in responses to temperature were stronger than responses to all environmental variables, with a more even mix of positive and negative correlations (Figure 4b). Correlations in responses to each environmental covariate can be found in Appendix S4, as can species individual responses to environmental covariates.

As previous research has suggested potential associations between commonly occurring cool-water species (pike, perch, roach, whitefish) and cold-water species (brown trout and Arctic charr), these associations are shown in more detail in Figure 5, with thermal guild classifications found in Table 3. The association between brown trout and Arctic charr was negative at lower temperatures, becoming gradually positive before peaking at the mean temperature and decreasing as temperatures further increased. Arctic charr associations with perch, pike and roach were all negative at the lowest temperature, remained such until the mean temperature, and then increased slightly to be around neutral at higher temperatures. Arctic charr associations with whitefish increased consistently from being negative at the lowest temperature, before levelling out and remaining neutral at higher temperatures. Brown trout associations with perch, pike and roach all followed similar patterns, with

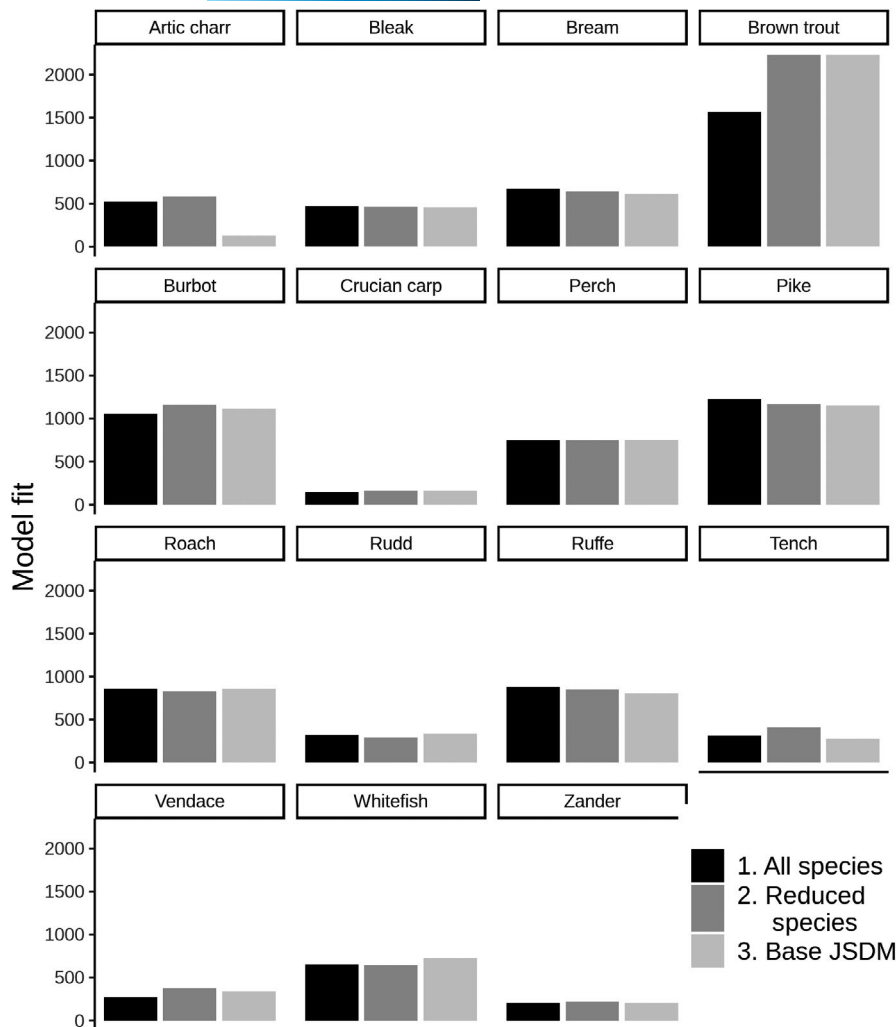


FIGURE 2 Model fit for three joint species distribution models mapping freshwater fish associations across 3308 Fennoscandian freshwater lakes. Model one utilises data from every species available, whereas model two utilises only data from species which occurred in over 10% of lakes. Models one and two estimate changes in species associations over a temperature gradient. Model three is a basic JSDM which monitors species associations, but does not estimate changes in associations over a temperature gradient. Model fit was measured using the improvement of each model's deviance values over the deviance values given by a stacked species distribution model which did not account for associations between species

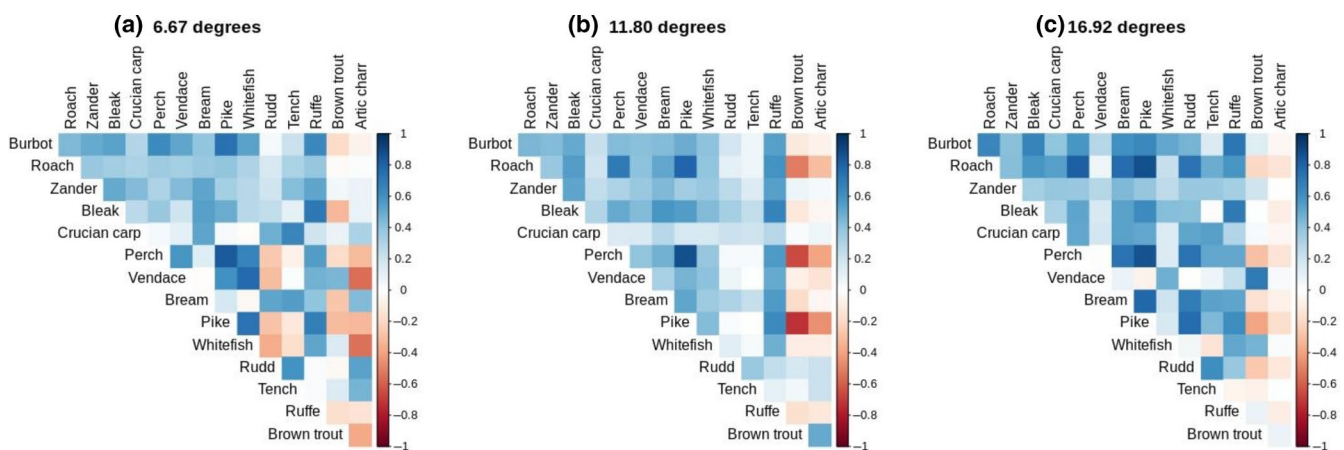
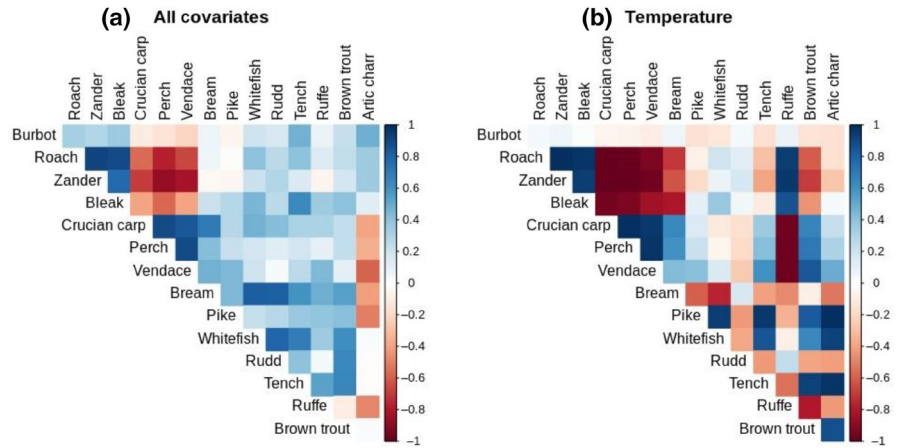


FIGURE 3 Estimates of associations between 15 different freshwater fish species across freshwater lakes in 3308 lakes across the Fennoscandia region at different temperatures. Associations are shown for the region's (a) minimum (6.67 degrees), (b) mean (11.80 degrees) and (c) maximum (16.92 degrees) temperatures. Temperatures used represent average surface temperature during the warmest quarter of the year. Associations vary between 1 (most positive) and -1 (most negative)

associations close to neutral at the lowest temperature, becoming negative at the mean temperature and re-ascending towards zero as temperatures further increased. Associations between whitefish and brown trout were weakly positive at low temperatures, decreasing

to weakly negative at the mean temperature before becoming more positive at higher temperatures. Whitefish associations with pike, perch and roach were positive at lower temperatures, and became weaker (although still positive) at higher temperatures. Associations

FIGURE 4 Correlation due to shared environmental response of 15 different fish species across 3308 freshwater lakes in Fennoscandia. Figures show correlation due to response to (a) all environmental covariates used in the Joint Species Distribution Model and (b) average surface air temperature of the warmest quarter of the year. Associations vary between 1 (most positive) and -1 (most negative)



between perch, pike and roach were all strongly positive, with little variation across temperature.

Maps visualising modelled predictions of likely changes in freshwater species distributions can be seen in Appendix S5.

4 | DISCUSSION

The ability to predict changes in species associations over environmental gradients will be crucial to incorporate into species distribution modelling as climate change modifies temperatures (Freeman et al., 2018). Here, we quantify changes in species associations over a climate gradient on a multi-national scale, using a presence-absence data set comprising 3308 lakes to fit a series of JSDMs of different freshwater fish species.

In accordance with Tikhonov et al. (2017) we demonstrate that large-scale presence-absence data are capable of shedding light on species associations over environmental gradients. Species belonging to cold-water guilds are generally negatively associated (and thus have a low likelihood of co-occurrence) with species from warmer thermal guilds, and these associations may change as temperatures warm.

Our confidence in these results is boosted by the fact that many of the associations predicted by our model corroborate previous research performed on pairwise associations. The negative associations between the two cold-water species and the cool-water species included here have been observed on smaller scales in this and similar study regions (Byström et al., 2007; Hayden et al., 2017; Hein et al., 2013; Winfield et al., 2008). Likewise, some of the positive associations shown among cool-water species here also have historical precedence (Eklöv & Hamrin, 1989; Mills & Hurley, 1990; Sharma & Borgström, 2008).

A positive association between two species does not imply the lack of a negative impact of one species on another. Our results indicate a positive association between whitefish and perch, despite past evidence suggesting that whitefish are negatively impacted by the presence of perch (Hayden et al., 2013). However, it is possible for the two species to co-occur, e.g. through niche segregation (Hayden et al., 2014). However, since our response variable is binary,

significant impacts on habitat use or life-history would not necessarily equate to a demonstrable negative impact in this study unless one species were driven to local extinction, unlike when fitting a latent variable model to abundance data.

It is important to note that predictions of species associations may become uninformative at certain temperatures. For example, when temperatures reach levels that preclude a species occurring in that region at all, any effect of species associations in an environmental context becomes void (Tikhonov et al., 2017). This is reflected in the associations between some species of different thermal guilds, which are predicted to increase towards zero as temperatures reach the higher ends of the spectrum. Summer temperatures in the region's warmer lakes are higher than the temperature range of lakes typically occupied by cold-water species (Mandeville et al., 2019). As such our predictions of associations between species should only be considered reliable at temperature ranges where both species are capable of persisting independently.

Although such models are capable of estimating future shifts in community composition in response to climate change, we recommend instead treating estimates provided by such models as indications of potential larger trends and – similar to Wagner et al. (2020) – as a basis for generating hypotheses and focussing future research (Zurell et al., 2020). Although some of the associations here match previous research, others point to new potential threats to native cold-water species like the Arctic charr and brown trout, which should be studied more thoroughly. Although it was beyond the scope of this paper, further research could also take into account possible interactions between temperature and other environmental covariates, for instance habitat area, as research has suggested that often colder-tolerant species can withstand potential competition if there is enough available habitat and niche segregation within a given habitat patch (Hein et al., 2013).

These results show that on a broad, multi-national scale, shifts towards communities dominated by species which have higher thermal tolerance are likely to occur as climate change drives average temperatures higher. Although many lakes may not reach the thermal maximum of native species, our model confirms that local extinctions are likely to occur earlier, driven by changing associations between native species and either invasive non-native species,

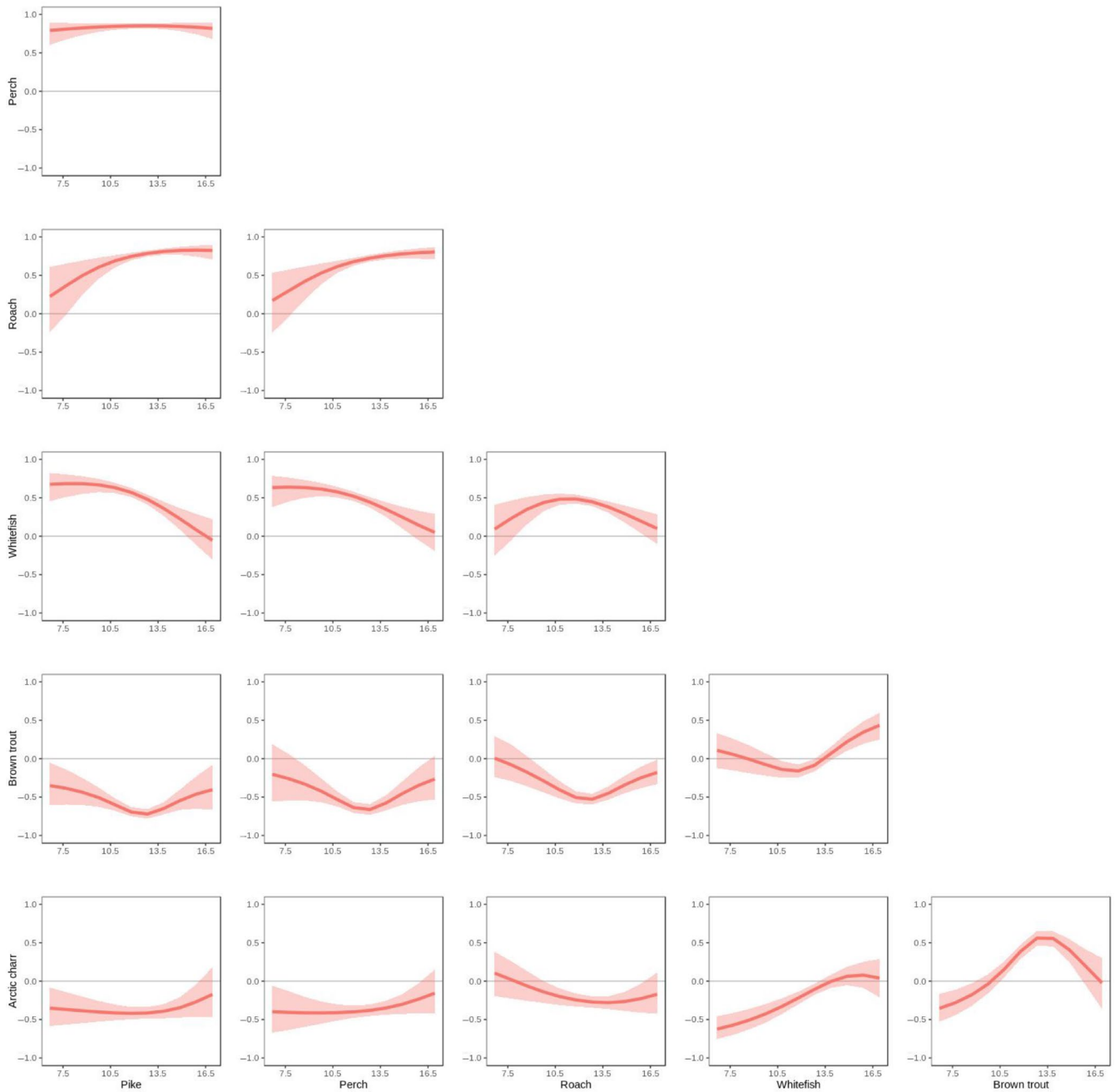


FIGURE 5 Associations between six freshwater fish species over a temperature gradient inferred from residual correlations from a joint species distribution model across 3308 freshwater lakes in the Fennoscandian region. Temperatures displayed on x-axes represent average surface temperature during the warmest quarter of the year. Associations are displayed on y-axes on a scale from -1 to 1, with ribbons representing 95% credible intervals. Negative values represent negative associations between species

Common name	Thermal guild	References
Perch	Cool	Hayden et al. (2014); Hokanson (1977)
Pike	Cool	Wehrly et al. (2003)
Roach	Cool	Elliott (2010)
Whitefish	Cool-cold	Hayden et al. (2014)
Brown trout	Cold	Elliott (2010); Wehrly et al. (2003)
Arctic charr	Cold	Elliott (2010)

TABLE 3 Thermal guild classification of six freshwater fish species surveyed in 1995 Nordic Fish Status Survey, with references citing precedent for classification

range shifting species or species with which native fish had previously co-occurred. The tendency of many species towards positive associations with an increase in temperature suggests a trend towards homogenisation of freshwater communities, though a variation in species individual responses to increased temperature could affect this.

Previous research indicates that more cold-tolerant species are capable of persisting in larger, deeper lakes due to the possibility of spatial segregation (Hein et al., 2013). Areas with strong topographical variation could provide dispersal barriers for novel species, and subsequently provide refugia for species likely to be outcompeted (Perrin et al., 2020). However such refugia are only likely to be tenable if human translocation is sufficiently regulated so as to prevent the introduction of novel species (Hesthagen & Sandlund, 2004; Perrin et al., 2021). As such, models like the one constructed here could enable researchers not only to identify environmental covariates which may drive changes in species associations and subsequently identify areas where native species are vulnerable to local extinctions, but also to identify areas where such species are likely to persist.

The ability of large-scale SDMs to predict changes in species associations while corroborating smaller-scale pairwise research over a temperature gradient is encouraging. It implies that large-scale presence-absence data may be capable of predicting changes in community composition as temperatures increase in the coming decades. Although much work remains to ensure the accuracy and reliable management application of such models, our results here indicate that JSDMs can be used to identify the potential impacts of climate change and range-shifting species on global ecosystems.

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CONFLICT OF INTEREST

No conflict of interest for the article.

DATA AVAILABILITY STATEMENT

Data and code used for the species distribution modelling are archived in Zenodo at <http://doi.org/10.5281/zenodo.4665778>.

ORCID

Sam Wenaas Perrin  <https://orcid.org/0000-0002-1266-1573>

Bert van der Veen  <https://orcid.org/0000-0003-2263-3880>

Nick Golding  <https://orcid.org/0000-0001-8916-5570>

Anders Gravbrøt Finstad  <https://orcid.org/0000-0003-4529-6266>

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