

Dispersal through stream networks: modelling climate-driven range expansions of fishes

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ABSTRACT

Aim To incorporate dispersal through stream networks into models predicting the future distribution of a native, freshwater fish given climate change scenarios.

Location Sweden.

Methods We used logistic regression to fit climate and habitat data to observed pike (*Esox lucius* Linnaeus) distributions in 13,476 lakes. We used GIS to map dispersal pathways through streams. Lakes either (1) contained pike or were downstream from pike lakes, (2) were upstream from pike lakes, but downstream from natural dispersal barriers, or (3) were isolated from streams or were upstream from natural dispersal barriers. We then used climate projections to model future distributions of pike and compared our results with and without including dispersal.

Results Given climate and habitat, pike were predicted present in all of 99,249 Swedish lakes by 2100. After accounting for dispersal barriers, we only predicted pike presence in 31,538 lakes. Dispersal barriers most strongly limited pike invasion in mountainous regions, but low connectivity also characterized some relatively flat regions.

Main conclusions The dendritic network structure of streams and interconnected lakes makes a two-dimensional representation of the landscape unsuitable for predicting range shifts of many freshwater organisms. If dispersal through stream networks is not accounted for, predictions of future fish distributions in a warmer climate might grossly overestimate range expansions of warm and cool-water fishes and underestimate range contractions of cold-water fishes. Dispersal through stream networks can be modelled in any region for which a digital elevation model and species occurrence data are available.

Keywords

Bioclimate envelope models, climate change, connectivity, dispersal barriers, fish distributions, stream networks.

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INTRODUCTION

Global temperatures are rapidly increasing, with higher average temperatures in the Northern Hemisphere during the past 50 years than have likely occurred in at least the past 1300 years (IPCC, 2007). A variety of plants and animals have responded to this warming through changes in distribution, phenology, behaviour and morphology (Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Thomas *et al.*, 2006), and more dramatic changes might be expected given future climate projections.

Most predictions of future species distributions build bioclimate envelope models to fit observed species occurrence data to current climate conditions. Projected climate values are then substituted into the model to predict future species distributions (Pearson & Dawson, 2003; Heino *et al.*, 2009). This approach is based on the assumption that dispersal barriers do not limit species distributions (Pearson & Dawson, 2003; Huntley *et al.*, 2010). When this assumption is not met, range expansions of warm-adapted species might be exaggerated, whereas loss of habitat for cold-adapted species might be underestimated.

It is essential to include dispersal in models predicting range shifts, and this requires quantitative information on: (1) the distribution of barriers across the landscape and (2) the colonization capacities of individual species (Malcolm *et al.*, 2002; Huntley *et al.*, 2010). Most models that incorporate landscape fragmentation assume that organisms can only colonize contiguous, suitable habitat (Peterson *et al.*, 2002; Parra-Olea *et al.*, 2005). Some models incorporate migration rates by defining the number of grid cells an organism could move through per time step (Dullinger *et al.*, 2004; Midgley *et al.*, 2006); others calculate the probability of colonization as a function of the distance from the nearest source population (Engler & Guisan, 2009; Midgley *et al.*, 2010). The most complex models include measures of population dynamics (e.g., generation time and birth rate) in addition to landscape structure and colonization capacity (Dullinger *et al.*, 2004; Engler & Guisan, 2009; Midgley *et al.*, 2010). All of these models use a two-dimensional grid cell structure to represent the landscape. Organisms can colonize new grid cells in any direction as long as they move through areas of suitable habitat.

This two-dimensional landscape structure is often suitable for modelling range shifts of terrestrial plants and animals, but this structure will often fail when modelling freshwater organisms (Fagan, 2002). Unlike terrestrial organisms that can colonize suitable habitat in all directions, many freshwater organisms can only colonize new habitats by travelling through the network formed by streams and lakes (Fagan, 2002; Arnott *et al.*, 2007). Unique properties of landscape connectivity result from the dendritic structure of stream networks (Fagan, 2002; Grant *et al.*, 2007). First, lakes that are geographically close together might be far apart in terms of within-stream distances (Magnuson *et al.*, 1998; Arnott *et al.*, 2007). Second, the position of dispersal barriers within stream networks largely determines the connectivity of watersheds. Barriers positioned near the basal stem of a watershed will render entire upstream catchments inaccessible to fishes, whereas barriers near terminal nodes will not have a large effect on connectivity (Fagan, 2002). Third, most barriers are unidirectional, impeding upstream dispersal but not necessarily limiting downstream dispersal. Thus, the point of initial colonization largely determines how organisms will spread through stream networks (Adams *et al.*, 2001).

Consequently, it is crucial that models of dispersal in freshwater ecosystems use an explicit spatial representation of the network structure that includes the positions of barriers. Published studies that use climate projections to predict future fish distributions have not explicitly included the effects of dispersal barriers in stream networks (Eaton & Scheller, 1996; Sharma *et al.*, 2007; Buisson *et al.*, 2008). The objective of this study is therefore to demonstrate how dispersal barriers in stream networks can be included in models of future climate-driven invasions of native or exotic species. Specifically, we predict the future distribution of pike (*Esox lucius* Linnaeus) in Sweden with and without including dispersal. Both the distribution and productivity of pike populations are expected

to expand across the northern portions of their range (Reist *et al.*, 2006). We hypothesize that pike will expand northward and to higher elevations in Sweden given a warmer climate, but that barriers will limit pike expansion. Predicting changes in the distribution of this species is important because, as top predators, pike affect the distribution of a variety of species, including sticklebacks, cyprinids, salmonids and ducks (Bystrom *et al.*, 2007; Spens & Ball, 2008; Englund *et al.*, 2009; Dessborn *et al.*, 2010).

METHODS

Study area and organism

Sweden extends from 55 to 69° N and covers an area of 449,964 km². The climate is temperate to subarctic, with a mean annual air temperature of 8.0 °C and −2.2 °C in the southern and northernmost parts of Sweden, respectively (means from 1961–1990, <http://www.smhi.se/klimatdata/>). The mean annual air temperature in Sweden is predicted to be 2.5 °C warmer by 2050 and 4 °C warmer by 2100, with maximum mean summer (June–August) air temperatures in 2100 of 24 and 14 °C in the southern and northernmost portions of Sweden, respectively (SMHI, <http://www.smhi.se/klimatdata/>). Mountains span the north-western length of Sweden and reach 2111 m above sea level at the highest point. Nearly all major rivers in Sweden flow from the mountains into the Baltic Sea in the east. The country is lake rich, with at least 100,000 lakes for which data are available and an estimated 227,000 lakes larger than 0.001 km² (Håkanson, 1994). Most lakes are oligotrophic or mesotrophic and are weakly acidic (Bergström *et al.*, 2005). Acidification caused the extirpation of fishes from lakes in Sweden, but many fish populations have now recovered (Appelberg, 1998).

The glacial history of lakes in Sweden is important for understanding fish distributions throughout the country. Since the most recent deglaciation in Sweden, c. 13.5–13.0 thousand years before present (kyr BP), the Baltic Sea has gone through several freshwater and marine stages, with Ancylus Lake (c. 9.5–8.0 kyr BP) being the largest freshwater lake to occur in the region (Björck, 1995). Ancylus Lake included the modern Baltic Sea in addition to much of coastal and central Sweden (Björck, 1995) and allowed widespread dispersal of fishes across Fennoscandia (Nordqvist, 1903). Much of Sweden continues to experience isostatic rebound, with land rising as much as 5–9 mm per year in the north (Englund *et al.*, 2009). The northern Baltic Sea, of low salinity (2–4‰) tolerable to most freshwater fishes, serves as a colonization source for inland lakes, many of which were once bays of the sea (Englund *et al.*, 2009).

Pike are among the cool-water guild of fishes (Eaton & Scheller, 1996), and their optimal temperature for growth is c. 20 °C (Casselman, 1996). Pike are tolerant to a wide range of water temperatures (< 29.4 °C), dissolved oxygen levels (> 1.5 mg L⁻¹ if temperature is 28 °C) and pH values (5–9.5) (Casselman, 1996). Pike are native to Sweden, and

their distribution is limited by connectivity rather than by local factors such as lake morphology or water chemistry (Spens *et al.*, 2007). Pike are absent from isolated lakes and lakes upstream from channel slopes steeper than *c.* 7% (Spens *et al.*, 2007). As top predators, pike strongly influence many prey species distributions, but pike distributions are not limited by other fishes (Craig, 1996; Magnuson *et al.*, 1998; Spens & Ball, 2008; Englund *et al.*, 2009). Pike can even survive in lakes without other fish species by feeding on macroinvertebrates and on each other (Casselman, 1996; Beaudoin *et al.*, 1999).

Pike occurrence data

We used a database that includes occurrence records of 55 fish species in lakes across Sweden. This database is a compilation of governmental records and interviews of private citizens conducted by Göran Englund and others at Umeå University. Governmental records include monitoring reports, fisheries management activities (e.g., treating lakes with rotenone, a piscicide, to extirpate unwanted fishes, stocking desirable fishes) and mailed surveys.

From this database, we compiled data on pike presence–absence in lakes across Sweden. Pike presences included all lakes where pike were observed present between 1800 and 2008 and remained present after documented rotenone treatments. Pike absences only included lakes that did not have a single record of pike presence and that incorporated interview and/or archival data. Monitoring alone did not constitute a pike absence because pike are often missed in gill nets and other sampling gear. Our final data set included 13,476 pike presence–absence records.

Lake morphology and pH

We used a Geographic Information System (ARCGIS 9.3; ESRI Inc., Redlands, CA, USA) to calculate the areas of 99,249 lakes (range 0.0003–5519.2 km²). Among lakes with pike presence–absence data, the mean area was 2.13 km² and the range was 0.0009–5519.2 km². We extracted pH data from a water chemistry database that includes data from governmental archives and research at Umeå University. We used the minimum pH value recorded for each of 3511 lakes with pike presence–absence data (mean = 6.3, range = 4.0–9.3).

Climate data

We obtained climate predictions of Sweden from the Rossby Centre regional atmospheric climate model (RCA3) (Kjellström *et al.*, 2005), which used boundary conditions from the global climate model ECHAM4/OPYC3 (Roeckner *et al.*, 1999). The RCA3 model used observed concentrations of greenhouse gases from 1961 to 1990 and simulated greenhouse gas concentrations from 1991 to 2100 (A2 and B2 emissions scenarios). The B2 scenario resulted in lower future concentrations of greenhouse gases than the A2 scenario, but higher

concentrations than predicted by the most conservative (B1) of the Intergovernmental Panel on Climate Change (IPCC) scenarios (Nakicenovic & Swart, 2000; IPCC, 2007). Climate predictions were at a monthly resolution from 1961 to 2100 on a 50 × 50 km grid (<http://www.smhi.se/klimatdata/>). We extracted ten different temperature measurements, but as they were all highly correlated, we only used mean annual air temperature as a predictor of pike distributions. We averaged simulated temperature data from 1961 to 1990 to represent current climate conditions and averaged data from 2046 to 2055 and from 2091 to 2100 to represent climate conditions during two periods in the future. The latter time period used the future-most simulation data available and represented the most extreme change. The former time period allowed us to investigate how much change might be expected in the nearer future.

Connectivity of stream networks

We used ArcGIS 9.3 in conjunction with pike occurrence data to map the potential for pike invasion as a function of lake connectivity. We classified 99,249 Swedish lakes as one of the following: (1) currently contains pike and/or is downstream from a lake that contains pike (observed pike network), (2) upstream from and connected to the observed pike network, but downstream from natural dispersal barriers (accessible), (3) isolated from the stream network or upstream from natural dispersal barriers (inaccessible). The procedure used to classify lakes is presented in a schematic diagram (Fig. 1) and is fully described in Appendix S1 in Supporting Information.

A channel slope $\geq 6.4\%$ was defined as a natural dispersal barrier for pike (see Appendix S1) and was similar to that of an independent study, which defined slopes $\geq 6.6\text{--}7.0\%$ as dispersal barriers for pike (Spens *et al.*, 2007). We determined the slope threshold by observing whether pike recolonized 114 lakes in Sweden that had been treated with rotenone, a piscicide. Rotenone treatments on these lakes occurred between 1930 and 1980, with most treatments occurring in the 1960s. Pike presence or absence was observed 10–64 years later (average 39 years) in each of the 114 lakes between 1976 and 2009 (most sampling events occurred after 2001). This time span is comparable to the time spans (40 and 90 years) over which we model pike dispersal in this study. Still, over longer time periods (thousands of years), fishes have dispersed across watershed boundaries and other barriers (Boizard *et al.*, 2009).

Modelling observed pike distribution

We fit logistic regression models to observed pike presence–absence data using various combinations of mean annual air temperature (hereafter air temperature), lake area, natural dispersal barriers and pH as predictors (Table 1). We needed to use some of the pike presences to map the observed pike

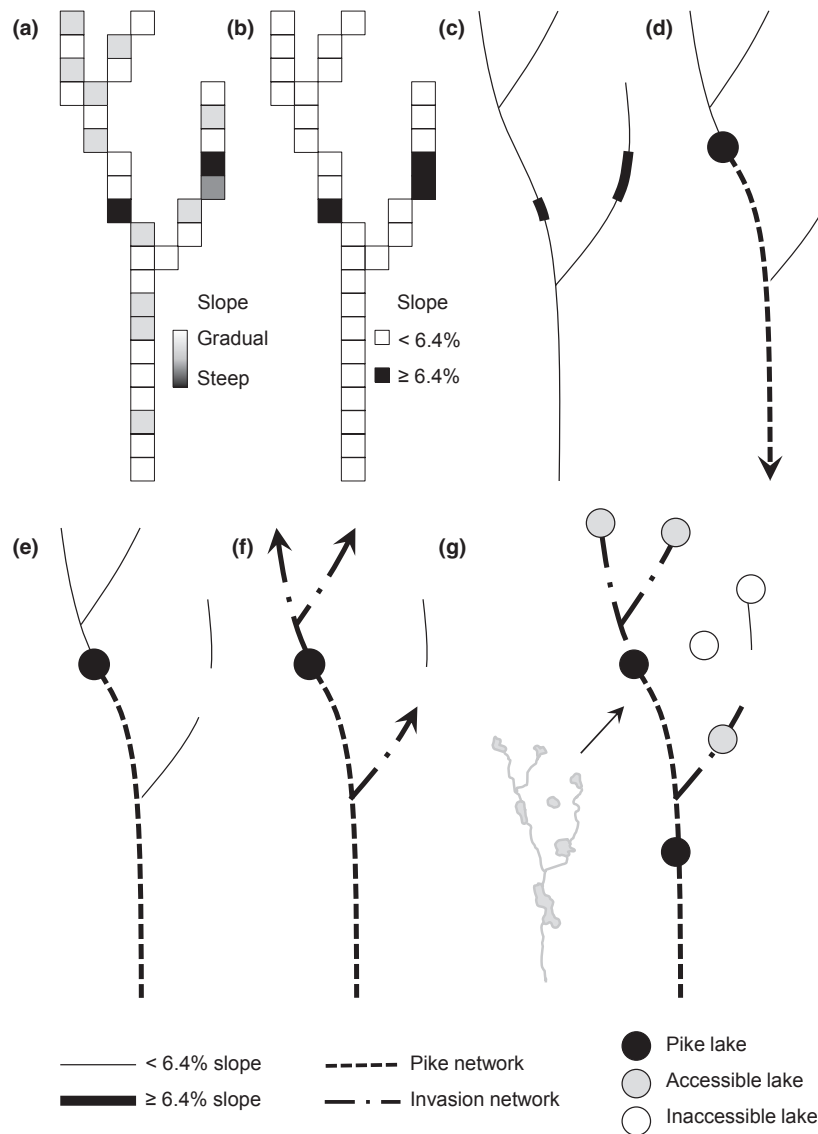


Figure 1 Schematic diagram showing the method used to determine the connectivity of lakes in Sweden and map potential pike (*Esox lucius* Linnaeus) invasion pathways (see Appendix S1 for full description). (a) First, we created a stream raster using a 50-m digital elevation model (DEM) and calculated slopes between contiguous cells along the stream path. (b) Second, we classified slopes as $\geq 6.4\%$ or $< 6.4\%$. (c) Third, we converted the stream raster file to a polyline shapefile, with separate stream segments for slopes $< 6.4\%$ or $\geq 6.4\%$. (d) Fourth, we created an observed pike network by tracing downstream (depicted by the downward pointing arrow) from each of the 9748 lakes documented to contain pike. (e) Fifth, we deleted all stream segments with slopes $\geq 6.4\%$ from the stream network, but not from the observed pike network. (f) Sixth, we traced upstream (depicted by the upward pointing arrows) from the observed pike network. The invasion network included all streams connected to the observed pike network that were also downstream from 6.4% slopes. We assumed barriers downstream from observed pike presences did not inhibit invasion because there were already source populations upstream. (g) Last, we classified lakes based on their connectivity with each of three networks. We used a polygon shapefile of 99,249 lakes to determine whether the lakes intersected (were within 100 m of) the stream networks (depicted by the grey map of lakes and streams). Pike lakes intersected the observed pike network. Accessible lakes only intersected the pike invasion network. Inaccessible lakes were either isolated from streams or intersected the stream fragments that were upstream from 6.4% slopes.

network (Fig. 1) and ultimately create the predictor variable describing natural dispersal barriers (1 designated accessible lakes and 0 designated lakes inaccessible to pike). We overrode barriers downstream from observed pike presences because these lakes could serve as source populations for invasion. However, we could not use the same pike presence observa-

tions both to define a predictor variable and to serve as a response variable in the logistic regression models. Therefore, we randomly selected 4000 pike presence observations to define the observed pike network (see Fig. 1) and categorize lakes as upstream or downstream from natural dispersal barriers.

Table 1 Model selection using Akaike's information criterion (AIC). Models within 2 AIC units of the minimum AIC had substantial support. Predictor variables used in the models included: lake area, mean annual air temperature, the relative position of lakes and dispersal barriers, and the minimum pH observed in a lake. Data set B was a subset of data set A because pH data were available for fewer lakes.

Model	Δ AIC
Data set A	
Area, temperature	1358.6
Temperature, barrier	23.4
Area, temperature, barrier	0.0
Data set B	
Area, temperature	805.0
Area, temperature, barrier, pH	1.0
Temperature, barrier	1.0
Temperature, barrier, pH	0.0
Area, temperature, barrier	0.0

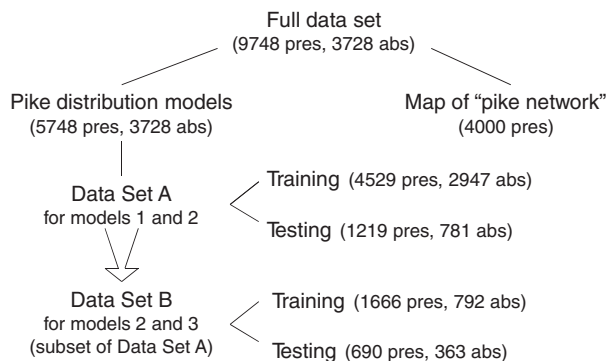


Figure 2 Diagram summarizing the use of pike presence-absence data for mapping connectivity between lakes, parameterizing pike distribution models (training set), and testing model performance (testing set). Data set B included pH data as a predictor variable, which was only available for a subset of the data. 'pres' refers to pike presence and 'abs' refers to pike absence.

We used the remaining 9476 observations of pike presences and absences (data set A) to build and test the logistic regression models (Fig. 2). Because pH data were not as widely available as physical data, fitting models that used pH as a predictor severely reduced the number of lakes available for data analysis. Therefore, we used two data sets to build the logistic regression models (Fig. 2). Data set A was used to build models that did not include pH, and data set B (a subset of data set A) was used to build models that did include pH. We used Akaike's information criterion ($AIC = L + 2m$, where m is the number of free parameters used in the model) to determine which models performed best within each data set (Burnham & Anderson, 2002). This metric calculates the likelihood of the data given each model, but chooses the most parsimonious model by penalizing each additional parameter with an added constant

(Burnham & Anderson, 2002). Thus, the best of many competing models minimizes the AIC. We used the 'glm' library in R version 2.10.1 (R Development Core Team, 2009) and specified a binomial distribution and a logistic link function to fit the logistic regression models. Pike presences were predicted to occur when the probability of occurrence was > 0.5 .

Because pH did not improve model fit (Table 1), we only evaluated model performance using data set A. We divided data set A into a training set and a testing set (Fig. 2). The training set was used to parameterize the models, and the testing set was used to evaluate model performance (see Fielding & Bell, 1997). The testing set was used to calculate model performance statistics, which included overall percent correctly classified, sensitivity (percent presences correctly classified), specificity (percent absences correctly classified), Cohen's kappa and area under the curve (AUC). Percent correctly classified, sensitivity and specificity tend to be correlated with species prevalence, but both kappa and AUC are independent of species prevalence (Manel *et al.*, 2001). Kappa measures the proportion of observations correctly classified as present or absent while also accounting for chance (Manel *et al.*, 2001). Kappa values of 0.8–1.0 indicate very good model performance, 0.6–0.8 good, 0.4–0.6 moderate and 0.0–0.4 fair (Manel *et al.*, 2001). The probability threshold used to predict occurrence tends to be correlated with Kappa (Fielding & Bell, 1997; Manel *et al.*, 2001). AUC provides a measure of model performance across the full range (0–1) of probability thresholds used to predict occurrence and is therefore independent of both species prevalence and the probability thresholds (Fielding & Bell, 1997; Manel *et al.*, 2001). To obtain AUC, one plots the false positive fraction (1-specificity) against the true positive fraction (sensitivity) for all probability thresholds and then calculates the AUC (Fielding & Bell, 1997). An AUC value of 0.5 indicates that the model performs at random, AUC values of 0.7–0.9 indicate useful applications, and AUC values > 0.9 indicate high accuracy (Manel *et al.*, 2001). We used the ROC library in R to calculate AUC for each model (Sing *et al.*, 2005).

Modelling future pike distribution

We predicted future pike distributions with and without incorporating natural dispersal barriers at two periods in time: 2046–2055 and 2091–2100. To predict future pike distributions without accounting for barriers, we predicted pike occurrence in 99,249 lakes using the logistic regression model based on lake area and air temperature (model 1). We also used model 1 to predict future distributions given barriers, but forced inaccessible lakes to be absences. This allowed us to create an observed pike network based on all pike presences in our database and more fully map lakes that would be inaccessible to pike invasion. The count of predicted pike invasions did not include lakes along the observed pike network and/or lakes predicted to contain pike between 1961 and 1990. We did not

Table 2 Model performance metrics of logistic regressions predicting pike (*Esox lucius* Linnaeus) presence or absence in Sweden using data set A. Predictor variables used in the models included: lake area, mean annual air temperature, and the relative position of lakes and dispersal barriers.

Model	Sensitivity	Specificity	PCC	Kappa	AUC
Area, temperature (1)	83	38	66	0.23	0.70
Area, temperature, barrier (2)	84	66	77	0.51	0.84

PCC, percent correctly classified; AUC, area under the curve.

use pH to predict future pike distributions because pH did not substantially improve model performance.

RESULTS

Models

Both air temperature and barriers were essential variables to include in models predicting pike presence–absence, but pH was not. Although models that included pH had low AIC values and were among the top-performing models, simpler models that did not include pH performed just as well (Table 1). Because pH data are not as widely available as lake area, air temperature and lake position in relation to barriers, we fit models using the full data set (A) without pH. A model composed of lake area, air temperature and barriers performed best; all two-variable models had substantially higher AIC values (Table 1).

The logistic regression models predicting pike presence–absence using data set A were:

$$P = -0.65 + 0.070a + 0.28t \quad (1)$$

$$P = -1.5 + 0.029a + 0.29t + 2.0b \quad (2)$$

where P is the probability of pike presence, a is lake area (km^2), t is average annual air temperature ($^{\circ}\text{C}$) and b is a dummy variable for barriers. The same models were produced by the A2 and B2 emissions scenarios of average annual air temperatures from 1961 to 1990. Model 2 performed much better than model 1 because barriers were added as a predictor in model 2 (Table 2). Model 1, based on lake area and air temperature only, had a fair kappa value and an AUC value bordering the cut-off for useful applications. The sensitivity of model 1 was high, but the lack of ability to correctly classify pike absences made overall model performance fair. Adding a barrier predictor to the model improved specificity and overall model performance, with kappa indicating moderate performance and AUC indicating a useful model (Table 2).

Predictions

The number of lakes expected to contain pike by 2100 was vastly fewer after mapping which lakes were inaccessible to pike invasion (upstream from natural barriers, Fig. 3). By 2100, model 1 predicted pike presence in 100% of lakes in Sweden (Fig. 3b) regardless of which emissions scenario was used. After mapping barriers, only 31.8% of Swedish lakes were accessible to pike (Fig. 3c). Using the 6.4% slope threshold for barriers, we classified 39,731 lakes as isolated from streams, 27,980 lakes as upstream from barriers, and 31,538 lakes as

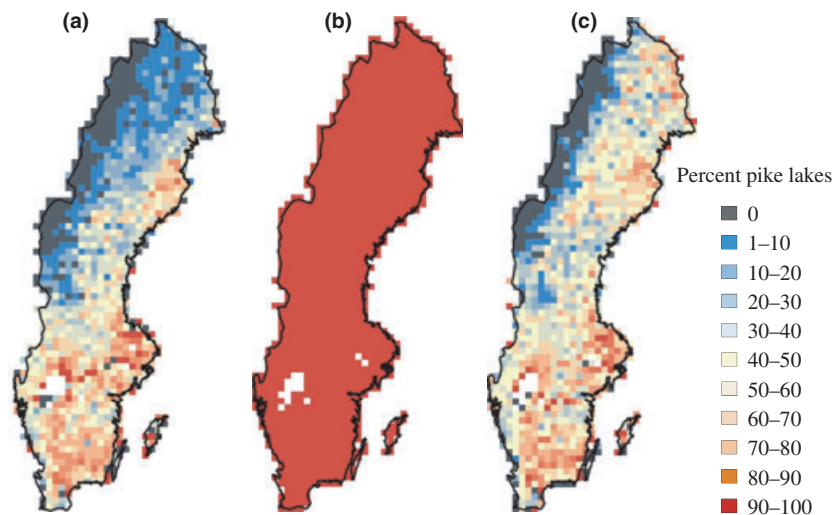


Figure 3 Pike (*Esox lucius* Linnaeus) distribution in Sweden as percent pike lakes within a 20×20 km grid. (a) The observed pike distribution included all pike present lakes predicted by the bioclimatic model (model 1) for the period 1961–1990 and all lakes within a 100-m buffer of the observed pike network. (b) The bioclimatic model predicted pike to be present in all Swedish lakes by 2091–2100. (c) After mapping dispersal barriers on top of bioclimatic model predictions, fewer lakes were predicted to contain pike by 2091–2100.

Table 3 Number of predicted pike (*Esox lucius* Linnaeus) invasions from 1991 to 2055 and from 2056 to 2100 given expected average annual temperatures in 2046–2055 and 2091–2100. The 'bioclimatic' model was based on predictions of a logistic regression model that included lake area and mean annual air temperature as predictors. 'Bioclimatic + barriers' used the same model, but did not include lakes mapped as isolated or upstream from a 6.4% slope as invadable. Lakes along the observed pike network and/or lakes predicted to contain pike between 1961 and 1990 were not included in the count of predicted pike invasions.

Model	2055	2100	Total
Bioclimatic	34,843	19,206	54,049
Bioclimatic + barriers	7011	2088	9099

downstream from barriers. Thus, we predicted that only 31,538 of 99,249 lakes will contain pike by 2100. Of those lakes, 9099 represented new invasions (Table 3).

We repeated the spatial analysis using slopes $\geq 7\%$ as barriers to pike dispersal (from Spens *et al.*, 2007) to determine how sensitive our results were to the slope threshold chosen. When we used a 7% slope threshold instead of a 6.4% slope threshold, 1478 more lakes were invadable. However, this resulted in only a 1.5% increase (from 31.8 to 33.3%) in the percent of all lakes that were accessible to pike.

With or without incorporating barriers into future predictions, most pike invasions will already occur by 2055, with fewer invasions during 2056–2100 (Table 3). Invasions will occur in the northern half of Sweden from 1991 to 2055 (Fig. 4a,c) and in the northern quarter of Sweden from 2056 to 2100 (Fig. 4b,d). If one accounts for barriers, invasions will not occur in the high mountains of western Sweden and fewer invasions will occur overall (Fig. 4a,b).

Natural dispersal barriers were more frequent and therefore, more important to incorporate into the pike range-shift model in hilly and mountainous terrain than in flat terrain (Fig. 5). We used the standard deviation of elevation (sde) from a 50-m resolution digital elevation model (DEM) within a 2500 km² area as a metric for relative hilliness. In hilly areas (sde > 15), 75–100% of lakes were inaccessible to pike and could erroneously be predicted to contain pike in the future. This proportion decreased to 23% in the flattest area (sde = 1.67), but the positive linear portion of the graph was highly variable. For example, 19–66% of lakes were inaccessible to pike in eight areas with sde between 3.15 and 3.97. Even in relatively flat terrain, connectivity of lakes can be important to incorporate into predictions of future pike distributions.

DISCUSSION

Our results show that it is essential to consider dispersal barriers when forecasting future fish distributions. Without incorporating dispersal through stream networks, we would have grossly overestimated the future distribution of pike in Sweden (Fig. 3). After mapping the positions of barriers along

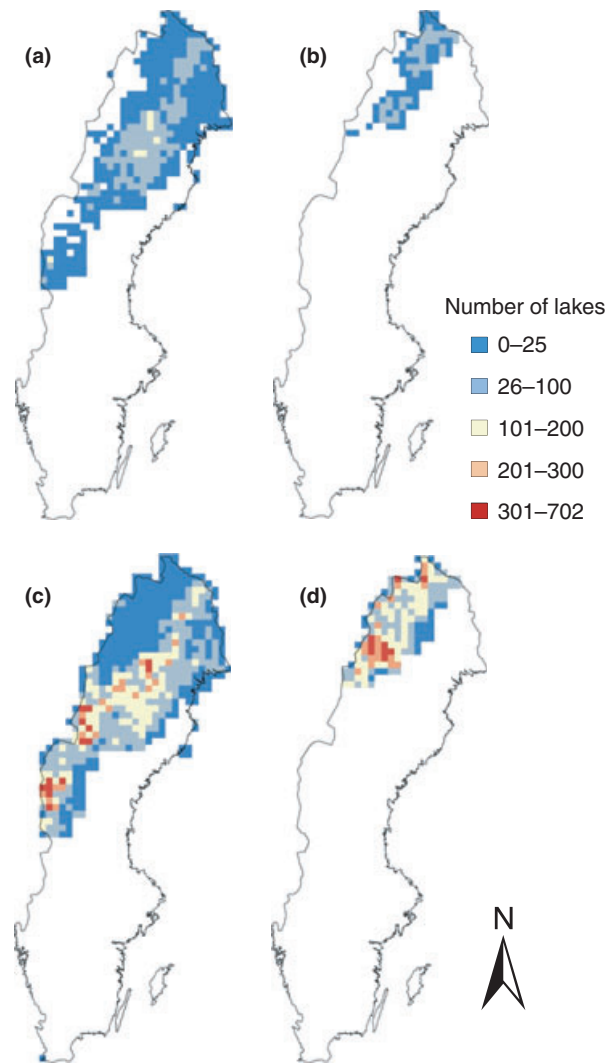


Figure 4 Number of lakes that pike (*Esox lucius* Linnaeus) were predicted to invade based on lake area and mean annual air temperature. Each map shows the number of invasions between (a) 1991 and 2055 in lakes downstream from natural barriers, (b) 2056 and 2100 in lakes downstream from natural barriers, (c) 1991 and 2055 in all lakes, and (d) 2056 and 2100 in all lakes. The maps do not include lakes along the observed pike network and/or lakes that were predicted to contain pike during the baseline time period (1961–1990). Each cell is 400 km².

the stream network in relation to pike source populations, we predicted 9,099 lakes to be invaded by pike by the year 2100 rather than 54,049 lakes (Table 3 & Fig. 4).

Although it is obvious that dispersal barriers are important to include in bioclimate envelope models in mountainous landscapes, we found that lake isolation can also be important in relatively flat landscapes (Fig. 5). Both steep stream gradients and lack of stream outlets serve as dispersal barriers to fishes and predominate in different types of landscapes (Magnuson *et al.*, 1998). For example, horizontal distance between lakes is the most important isolation variable for understanding fish communities in the kettle-lake landscape of

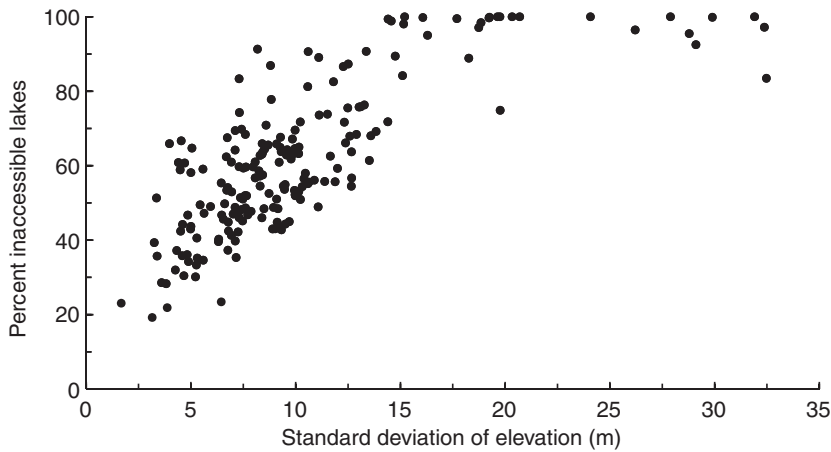


Figure 5 Percent of inaccessible lakes (isolated or upstream from a 6.4% slope) within 50×50 km areas given the relative hilliness of each area. A higher standard deviation of elevation (m) signifies more hilly terrain.

Wisconsin, whereas stream gradient is most important for distinguishing fish communities in relatively high-relief areas of Finland (Magnuson *et al.*, 1998).

Dispersal through stream networks can be modelled in any region for which a DEM and species occurrence data are available. The steepest downstream channel slopes are identified for all lakes with occurrence data, and a classification tree is then used to find the slope threshold that best defines barriers (Spens *et al.*, 2007). Observed absences indicate that fish were unable to colonize lakes over the long term. Therefore, the slope threshold serves as a barrier even during the times (e.g., spring floods) when the fish would be most able to pass steep slopes. Lakes with occurrence data used to define natural barriers must (1) not be downstream from any source lakes and (2) be suitable for the focal species to survive and reproduce. Mapping dispersal barriers will target areas where impacts of climate-induced invasions could occur and, conversely, areas where assisted migration of species endangered by climate change could be beneficial (McLachlan *et al.*, 2007).

Generating stream networks from a DEM produced realistic depictions of observed streams, but this process also generated error. We used a small catchment area (0.5 km^2) to define permanent streams. This threshold ensured that modelled streams reached lakes that were connected on a 1:50,000 scale map, but also generated small streams that did not exist on the map. Classification of lakes as inaccessible or accessible to pike differed among 28% of 214 lakes depending on which stream source (DEM versus map) was used. Coincidence of modelled and mapped streams might improve with a map and DEM of finer scale. This level of discordance might not be problematic for regional purposes, especially because error rates of classifying lakes as accessible or inaccessible were approximately equal. In addition, slope thresholds ranging from 6.4 to 7% did not dramatically alter our assessment of which lakes were accessible to pike invasion. However, management decisions for individual lakes should use on-site observations when possible. Maps do not fully depict dispersal routes (e.g., intermittent streams) or barriers (e.g., subsurface stream flow, man-made barriers) (Spens *et al.*, 2007). We did not account for these types of barriers, but additional barriers would result

in a more disconnected stream network with even less fish dispersal. For example, data from the Swedish Meteorological and Hydrological Institute show that 1881 of 4990 mapped dams in Sweden occur along the pike invasion network.

Models predicting habitat suitability for a given species over large regions must be fairly simple because few predictors generally have wide spatial coverage (Huntley *et al.*, 2010). Thus, these models rarely include all important habitat criteria. We successfully developed a model predicting pike occurrence based on three widely available variables: average annual air temperature, lake area, and natural dispersal barriers. This model (model 2) performed just as well as a more complex model (model 3) that included pH (Table 1). Other unmeasured variables (e.g., macrophyte cover within lakes or maximum depth) could be important for determining the success of pike populations (Casselman, 1996; Englund *et al.*, 2009), but our general predictions of future pike invasions in Sweden are robust. Pike populations have persisted in 47 of 49 lakes where pike have intentionally been introduced in the boreal region of central Sweden (Spens *et al.*, 2007). Given that a wide range of chemical and physical conditions characterized these lakes, Spens *et al.* (2007) suggest that connectivity rather than habitat is the primary factor limiting pike distributions.

Pike is a keystone predator and projecting future pike distributions will also be important for understanding how distributions of many other species will change. As top predators, pike have extirpated a wide range of fish species and generally have disparate distributions with the crucian carp (*Carassius carassius* Linnaeus), stickleback (*Pungitius pungitius* Linnaeus) and many species of salmonids (Byström *et al.*, 2007; Spens & Ball, 2008; Englund *et al.*, 2009). We expect extirpations of these species to occur in lakes that pike invade, but dispersal barriers will maintain refugia from pike predation in *c.* 68% of lakes throughout Sweden (Fig. 3). Biotic interactions could be incorporated into models predicting future distributions of salmonids and other species by using expected pike invasions to predict species extirpations.

Because human introductions of exotic species have become widespread across the globe (Hulme, 2009), some might render natural dispersal barriers obsolete. Indeed, humans have a long

history of stocking fishes valued for food (Nilsson, 1972; Adams *et al.*, 2001). The extent to which humans aid the dispersal process will depend both on the landscape and on the characteristics of the species. Northern latitudes are expected to experience the most extreme degree of warming (IPCC, 2007), but might be the least vulnerable to species introductions by humans. Boreal forests and arctic tundra harbour low human population densities (Small, 2004), thereby limiting the likelihood of human-assisted fish introductions to remote lakes (Magnuson *et al.*, 1998; Vander Zanden & Olden, 2008). Human population density or proximity to towns could be important predictors to include in range-shift models. Game fishes have been widely stocked in mountain lakes (Nilsson, 1972; Adams *et al.*, 2001), but introductions of nongame fishes are generally accidental. In Sweden, humans have both introduced pike to new lakes and extirpated pike from lakes to stock salmonids (Spens *et al.*, 2007). One cannot assume that humans will introduce pike into all lakes upstream from barriers.

Dispersal is important for structuring species distributions across the landscape, even in an era when human-assisted dispersal allows species to surmount natural barriers. Thus, incorporating dispersal into models predicting future species distributions given climate change is of utmost importance. We provide a method for modelling climate-driven range shifts that explicitly accounts for the dendritic network structure of freshwater ecosystems, an application that is critical for many freshwater organisms. Our results show that incorporating dispersal barriers in stream networks vastly reduces the predicted future range of pike in Sweden. Because pike are top predators and their invasion is likely to cause extirpation of other taxa, our results paint a much brighter picture of the future, with heterogeneity of pike occurrence maintained. In contrast, available habitat for cold-water species will likely contract even more dramatically than climate models alone project because remaining cold-water habitat will be at high altitudes and latitudes, both of which might be difficult to access (Hari *et al.*, 2006). We hope that the methodology we used to incorporate lake and stream connectivity into predictions of future fish distributions will be applied to other species in other systems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods to determine lake and stream connectivity and map potential pike (*Esox lucius* Linnaeus) invasion pathways in Sweden.

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