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Author for correspondence:
Catherine L. Hein
e-mail: clhein@gmail.com

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Fish introductions reveal the temperature dependence of species interactions

Catherine L. Hein[1,2], Gunnar Öhlund[2] and Göran Englund[2]

[1]Climate Impacts Research Centre, Abisko Scientific Research Station, 981 07 Abisko, Sweden
[2]Department of Ecology and Environmental Science, Umeå University, 901 87 Umeå, Sweden

A major area of current research is to understand how climate change will impact species interactions and ultimately biodiversity. A variety of environmental conditions are rapidly changing owing to climate warming, and these conditions often affect both the strength and outcome of species interactions. We used fish distributions and replicated fish introductions to investigate environmental conditions influencing the coexistence of two fishes in Swedish lakes: brown trout (*Salmo trutta*) and pike (*Esox lucius*). A logistic regression model of brown trout and pike coexistence showed that these species coexist in large lakes (more than 4.5 km^2), but not in small, warm lakes (annual air temperature more than 0.9–1.5°C). We then explored how climate change will alter coexistence by substituting climate scenarios for 2091–2100 into our model. The model predicts that brown trout will be extirpated from approximately half of the lakes where they presently coexist with pike and from nearly all 9100 lakes where pike are predicted to invade. Context dependency was critical for understanding pike–brown trout interactions, and, given the widespread occurrence of context-dependent species interactions, this aspect will probably be critical for accurately predicting climate impacts on biodiversity.

1. Introduction

Understanding and predicting the effects of climate change on ecosystems is a major focus of ecological research [1], yet a wealth of information about the character and strength of species interactions along environmental gradients has not been harnessed for predicting species responses to climate change.

The intensity and outcome of species interactions often depends on environmental conditions: competitive interactions between plants shift to facilitative interactions as environmental stress increases [2], the strength of top-down control in stream food webs varies with water temperature and hydrological regimes [3–4], and outbreaks of pathogenic fungi (*Batrachochytrium* sp.) are causing amphibian extinctions, largely because warming has increased the growth rate of the fungus [5]. The term context dependency refers to changes in species interactions that result from altered environmental conditions. Hence, to understand and predict the effects of climate change on species ranges, it will often be necessary to account for context dependency.

The past decade has seen an explosion in the number of species distribution models predicting climate-driven range shifts. These models use a suite of abiotic variables to describe the niche space where a species occurs and then superimpose future climate scenarios to make geographical predictions of range shifts [6]. The effects of species interactions are implicitly incorporated into bioclimate envelope models because they are fit to species' realized niches [6]. As exemplified by Leathwick [7], species distribution models can, in principle, be designed to account for interactions between abiotic and biotic factors (i.e. context dependency of species interactions), but this is rarely the case. Most studies include only the effects of abiotic factors [6], and if biotic factors are included, then it is their independent effects that are modelled [8–10]. Thus, models predicting climate-driven species range shifts generally do not account for context dependency of species interactions.

An additional weakness of species distribution models is that they describe present species–environment correlations, which do not necessarily reflect

causal relationships [1,6]. Spurious correlations will lead to erroneous predictions if changes do not occur in unison. Species may shift in abundance through space and time at different rates because they have different dispersal abilities and thermal sensitivities and use a variety of phenological cues [11]. In turn, interactions between coexisting species may change, and novel communities may form as extant species reshuffle or as species colonize new areas [11].

To accurately predict the effects of climate change on biodiversity under such conditions, it is essential that models are built on causal rather than on correlative relationships [1]. This requires controlled experiments performed at relevant spatial and temporal scales [12], but manipulating climate at the ecosystem scale is difficult or impossible in most settings. Instead, climate variables are often manipulated in the laboratory [3,13] or in field enclosures such as open-top chambers [14] or aquatic mesocosms [15]. Experiments of this type have been critical for developing causal relationships between climate and biological processes, but these studies may not be relevant for understanding ecosystem-level responses to climate change [16]. We argue that large-scale experiments (e.g. introductions of a new fish species to a lake) along environmental gradients are useful for studying the impacts of climate change on species interactions. Rather than manipulating environmental conditions, these experiments manipulate species assemblages and correlate the outcomes with environmental conditions. Here, causality is inferred for the species interaction, but not for the modifying effects of environmental variables.

In this study, we use fish introductions along environmental gradients to elucidate the effect of environmental conditions on biotic interactions. We first investigate how temperature affects coexistence between two fish species with different thermal performance curves. We then use our findings to predict how a warming climate will alter their future distributions. *Salmo trutta* (brown trout) are cold-water fishes with an optimal temperature for growth of 13.1–17.4°C [17], and *Esox lucius* (pike) are cool-water fishes with an optimal temperature for growth of *ca* 20°C [18]. Pike have strong, top-down effects on lake communities [19–21], but laboratory experiments suggest that their propensity to catch brown trout prey is minimal at low (less than 10°C) water temperatures [13]. We quantify a 'coexistence envelope' for brown trout and pike, i.e. the environmental conditions under which coexistence is observed, by contrasting observed presences of both fishes against the observed extirpation of brown trout following pike introduction. Second, we demonstrate how context dependency of species interactions can be incorporated into models that project species distributions under a warmer climate. We use the coexistence model coupled with temperature projections to predict how warming will affect brown trout populations in lakes where they coexist with pike today and in lakes where pike is expected to invade in the future.

2. Material and methods

(a) Study area and species

Sweden spans 55–69° N and its climate ranges from temperate to subarctic. The mean annual air temperature ranges from 8.0°C in the south to −2.2°C in the north (data for 1961–1990, http://www.smhi.se/klimatdata/). Climate scenarios across Sweden predict the mean annual air temperature to be 2.5°C warmer
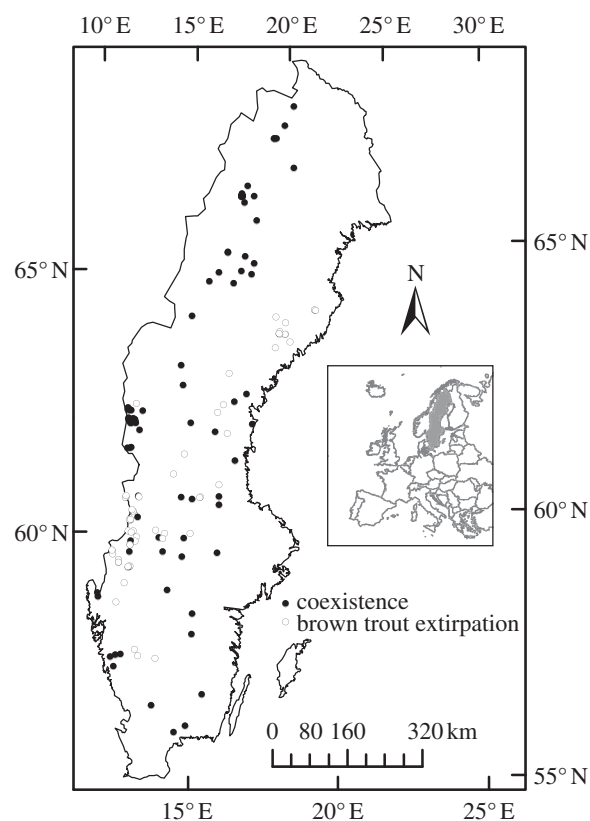

Figure 1. Map of lakes in Sweden included in the analysis of brown trout (*Salmo trutta*) and pike (*Esox lucius*) coexistence. Lakes where brown trout and pike coexist (black circles) were contrasted with lakes where brown trout were extirpated after pike introductions (open circles).

by 2050 and 4°C warmer by 2100 (http://www.smhi.se/klimatdata/). Physical data exist for at least *ca* 100 000 lakes in Sweden.

Brown trout are versatile in terms of their life-history and feeding behaviours. There are stream and lake-resident populations and migratory populations, which spawn in streams and migrate to larger rivers, lakes or the sea for feeding [22]. In lakes, brown trout often feed on benthic invertebrates and are likely to spatially overlap with pike, a littoral predator [23]. Brown trout are common prey for large pike [24] but reach a size refuge from pike predation at a total length of *ca* 37 cm [25]. Still, pike introductions to lakes often result in salmonid extirpations [19,21], and conversely, brown trout stocking is more successful in lakes where pike are rare or absent [21,26].

(b) Brown trout and pike occurrence data

To study the conditions under which brown trout and pike coexist, we compared lakes where the introduction of pike by humans has led to extirpation of brown trout ($n = 63$) with lakes where brown trout and pike coexist ($n = 88$, figure 1). Few cases of brown trout surviving pike introductions exist, and therefore, could not be used to characterize environmental conditions where coexistence occurs. The data were extracted from a database that includes records of 55 fish species in *ca* 18 100 lakes across Sweden. Data sources include governmental records (e.g. monitoring reports, stocking programmes, interviews and mailed surveys) and interviews with private citizens conducted by Göran Englund and others at Umeå University.

We used conservative criteria for coexistence in an attempt to eliminate brown trout presences from interview records that refer to stocking or to rare catches of stream-resident brown trout in connected lakes. To qualify as coexistence lakes, we required that both species were observed in gill net surveys in the same year or, if the information came from an interview, that the

Table 1. Median (minimum – maximum) values of lake predictor variables used in the logistic regression model that compared the presence ($n = 88$) or absence ($n = 63$) of brown trout–pike coexistence.

predictor variable	value
species number	5 (1–30)
maximum depth (m)	15.8 (2–221)
lake area (km^2)	0.73 (0.003–1886)
catchment area (km^2)	23.24 (0.16–12077)
elevation (m)	314 (16–846)
annual mean air temp. (°C)	3.09 (−2.14 to 7.3)

interviewed person had caught both species on the same date using gill nets or sport fishing gear. We excluded lakes with a history of brown trout stocking. Species data based on interviews can be error prone, but this dataset relies on the occurrence of two well-known sport fishes and is less likely than low-frequency fish surveys to falsely claim a species absence. Furthermore, an 'absence' in the data used to model coexistence is not an absence of either species, but a brown trout extirpation following a documented pike introduction by humans.

(c) Predictor variables

Six predictors of coexistence patterns were considered (table 1). The total number of species in each lake was included to represent alternate prey species, which might dampen the interaction between brown trout and pike. Maximum lake depth and lake area were included because cold water in the pelagic zone is more likely to occur in large, deep lakes and may provide a refuge from pike predation. Data on lake depth came from the national lake database (Swedish Meteorological and Hydrological Institute), questionnaires and interviews with local fishermen. We calculated the areas of lakes and their catchments using a geographic information system (ArcGIS 10.0; ESRI Inc., Redlands, CA, USA). Upstream catchment area served as a proxy for brown trout spawning habitat in streams in terms of relative stream length but not within-stream habitat. Elevations of lakes were extracted from the national digital elevation model (50×50 m grid), and mean annual air temperatures at lake outlets were obtained from a 50×50 km grid produced by the Rossby Centre regional atmospheric climate model (RCA3) [27]. We averaged simulated temperature data from the B2 emissions scenarios for three time periods: (i) 1961–1990, (ii) 2045–2055 and (iii) 2091–2100. Air temperatures from 1961 to 1990 were used to fit the logistic regression models. Annual mean temperatures in air and water are strongly correlated, although seasonal variation is more pronounced in small than in large lakes [28].

(d) Modelling brown trout–pike coexistence

The pike and brown trout data were used to model a coexistence envelope for the two species. We used logistic regression to model the 'presence' (brown trout and pike) or 'absence' (brown trout extirpation following pike introduction) of brown trout–pike coexistence. The full dataset was randomly divided into a training set to fit the models (61 presences, 45 absences) and testing set to evaluate model performance (27 presences, 18 absences). We used the glm library in R version 2.13.0 [29] and specified a binomial distribution and a logistic link function to fit the models. The full model included all six predictor variables and the following interaction terms: lake area × temperature, lake area × maximum depth and lake area × number of species. These three interaction terms represent our expectation that coexistence might depend
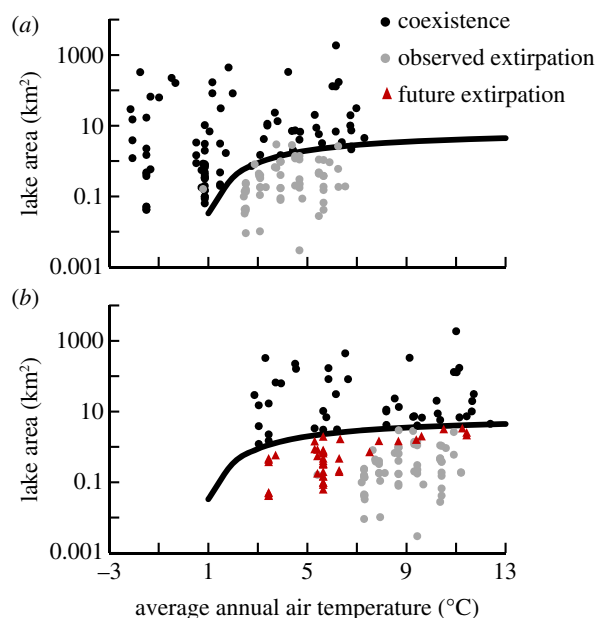

Figure 2. Patterns of observed and predicted brown trout–pike coexistence. The line in each graph plots the logistic regression model predicting coexistence (above the line) or brown trout extirpation (below the line). (a) Lakes with observed brown trout–pike coexistence and brown trout extirpations following pike introductions in terms of lake area and mean annual air temperatures averaged over 1961–1990. (b) Each lake is then plotted on the same graph using future air temperature projections (2091–2100). Brown trout will continue to coexist with pike in many lakes (black circles), but are also predicted to go extinct in lakes where they previously coexisted with pike (triangles). (Online version in colour.)

on having cold, pelagic habitat as refuge from pike predation or on having alternate prey species.

We built 42 models with various combinations of predictors from the full model and used Akaike's information criterion ($AIC = -2L + 2m$) to select the most parsimonious one. This criterion is based on the log likelihood of the data given the model (L) penalized for the number of estimated parameters (m) [30]. We calculated the following metrics on the testing data to assess performance of the best model: per cent correctly classified, sensitivity (per cent presences correctly classified), specificity (per cent absences correctly classified), kappa and area under curve (AUC) [31,32]. Coexistence was predicted whether the probability of 'presence' was greater than or equal to 0.5 as this threshold approximates the observed prevalence of coexistence in the dataset (0.58).

(e) Modelling future coexistence potential

We then used the best coexistence model to predict and map coexistence potential of brown trout and pike in lakes throughout Sweden for two time periods in the future: 2045–2055 and 2091–2100. Predictions were generated by substituting projected air temperatures into the best logistic regression model. We evaluated the future coexistence potential of brown trout and pike in 31 540 lakes that are predicted to contain pike in the future based on a pike distribution model [33].

3. Results

(a) Coexistence niche

Patterns of coexistence between pike and brown trout are well described by air temperature and lake area (figure 2a). The two

species coexist in cold lakes (mean annual air temperature less than 0.9–1.5°C) and in warm lakes if they are large (more than 1.2–4.5 km²). All lakes where pike were introduced, and caused subsequent trout extirpations were small and warm. The most parsimonious model predicting brown trout–pike coexistence included lake area, mean annual air temperature and the interaction between the two variables:

$$P = 5.59 + 0.15\,a - 6.15\,t + 0.92\,a^*t. \qquad (3.1)$$

Here, a is ln lake area (ha), t is mean annual air temperature from 1961 to 1990 (°C) and the probability of coexistence is $e^P/(1 + e^P)$. The five best models ranged in complexity, but the differences in AIC values were less than 2, meaning there was substantial support for all five models (see the electronic supplementary material, appendix S1) [30]. A more complex model had a lower AIC value than model 1, but this difference (0.23) was negligible (see the electronic supplementary material, appendix S1). Model 1 performed very well: the per cent correctly classified was 93.3%, the sensitivity was 96.2%, the specificity was 89.5%, kappa was 0.86 and the AUC was 0.99. Therefore, we used model 1 for our predictions of future brown trout–pike coexistence.

(b) Projected coexistence under climate change

Our models suggest that many small, cold lakes that currently contain both brown trout and pike will not provide for coexistence in the future because they will be too warm. In fact, we predict that trout extirpations will occur in nearly half of the lakes where they currently coexist with pike. Of 88 observed coexistence lakes in our dataset, 36 lakes are predicted to have trout extirpations by 2050 and seven more lakes by 2100 (figure 2b). The remaining lakes ($n = 45$) are large enough to provide for coexistence under warmer conditions in the future (figure 2b).

Scaling up to all lakes across Sweden, we estimated that 80% of present coexistence lakes will be vulnerable to brown trout extirpations in the future because warmer temperatures will push them outside of the coexistence envelope. This analysis was not based on observed fish data, which are not available for most lakes, but on predictions of pike–brown trout coexistence under present and future temperature scenarios. We first limited the analysis to 22 440 lakes in Sweden where pike were predicted to be present in 1961–1990 [33]. Second, we predicted that coexistence is possible in 3870 of these pike lakes based on the 1961–1990 temperatures. Third, we predicted that brown trout would be vulnerable to extirpation in 2750 coexistence lakes by 2055 and in 350 additional lakes during 2056–2100 (figure 3a). These extirpations are distributed throughout Sweden except the mountainous region in the northwest (figure 3a).

Climate-driven pike invasions will probably cause brown trout extirpations in many small, cold lakes that presently only contain brown trout. Given warming air temperatures and dispersal limitations, pike are predicted to invade 9100 Swedish lakes by the year 2100 [33]. Our coexistence envelope for brown trout and pike predicts that only 15 of these lakes will provide for coexistence in 2100 (figure 3b). Of the 7010 pike invasions predicted to occur by the year 2055, 6860 could cause trout extirpations (figure 4). All 2090 pike invasions predicted to occur between 2056 and 2100 would result in trout extirpations (figure 4).
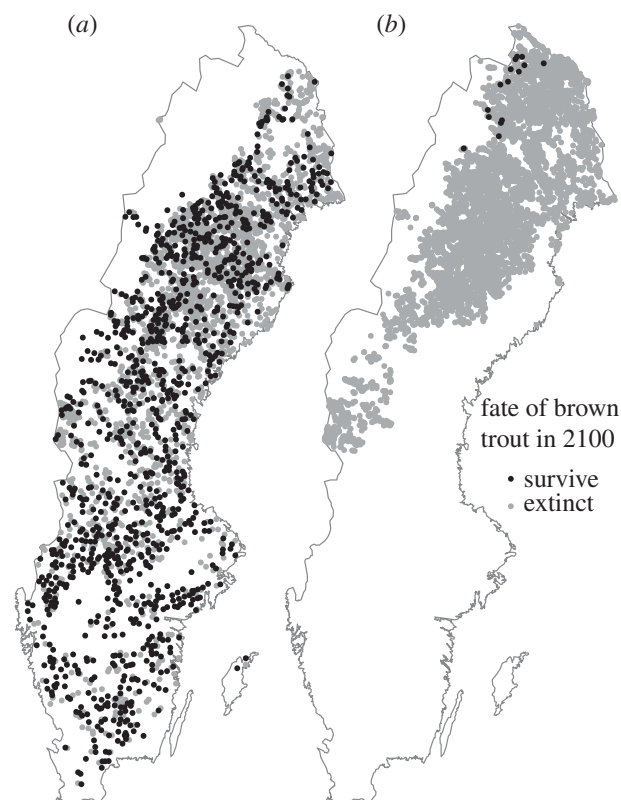

Figure 3. Future predictions (2091–2100) of pike–brown trout coexistence and brown trout extirpations in (a) lakes where pike and brown trout coexistence is possible under 1961–1990 temperatures, and (b) lakes where pike is predicted to invade. Only lakes where pike presence was predicted in 1961–1990 are included in (a).
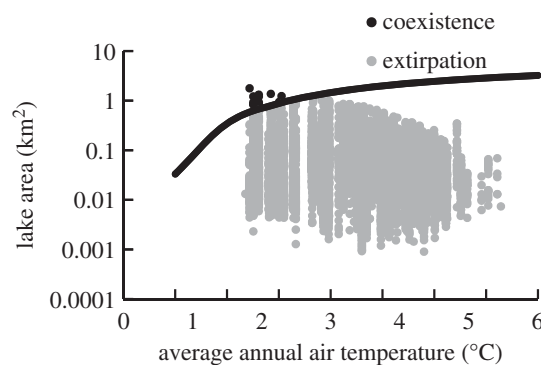

Figure 4. Future coexistence ($n = 15$) and brown trout extirpation ($n = 9084$) in lakes where pike is predicted to invade by 2100. The black line plots the logistic regression model predicting coexistence (above the line) or brown trout extirpation (below the line).

Despite the predicted future loss of suitable lakes for brown trout–pike coexistence, many lakes in Sweden will continue to support brown trout populations. By 2100, approximately 1720 large lakes will provide suitable habitat for coexistence. An additional ca 67 710 lakes in Sweden are inaccessible to pike invasion and thus can provide refugia for species such as brown trout [33].

4. Discussion

This study showed that coexistence of brown trout and pike depends on both lake area and temperature. The two species

coexist in cold but not in warm, small lakes (figure 2a). This is not because brown trout cannot tolerate higher temperatures; they are found in small pike-free lakes throughout southern Sweden. Our research suggests that they do not tolerate the high predation pressure from pike in warm, small lakes [13]. Pike are not as well adapted to cold conditions as brown trout [17–18], and experiments in large, artificial pools show that pike attack rates on brown trout decline by two orders of magnitude between 6°C and 10°C [13]. Although the precise mechanisms causing this pattern remain unknown, it is clear that brown trout outperformed its predator at low temperatures in these experiments [13]. Thus, interactions between pike and brown trout in small, warm lakes may be more intense owing to greater spatial overlap (e.g. no deep pelagic zone), higher attack rates and fewer alternate prey species. Conversely, lower attack rates by pike on brown trout and lower population size of pike may allow for coexistence in small, cold lakes.

Several mechanisms may explain why large lakes allow coexistence. Pike are littoral predators [23,34], and a deep, cold pelagic zone can therefore provide a refuge from pike predation. Moreover, the pelagic zone of large lakes often has abundant small-bodied pelagic prey species such as vendace (Coregonus albula), European smelt (Osmerus eperlanus) and dwarfed whitefish (Coregonus lavaretus) that allow brown trout to switch to a piscivorous diet, and thereby reach a size refuge from pike predation [13,35]. Small brown trout often occupy littoral habitat and then move offshore at larger sizes as they switch to a piscivorous diet, but the size at which this transition occurs varies (ca 15–36 cm length), and habitat use and diet vary on an individual basis [22]. The importance of predation risk in littoral versus pelagic habitat has been documented in other salmonids, with small Arctic char (Salvelinus alpinus) remaining in the littoral zone to avoid predation by large brown trout in the pelagic [36]. Additionally, larger habitat areas generally support larger populations that are less vulnerable to local extinctions caused by stochastic events [37].

The coexistence niche of brown trout and pike shows that biotic interactions can limit the large-scale distribution of a species. The idea that species distributions are constrained by biotic interactions has a long history in ecology [38–40] and was formalized by Hutchinson [41] as the contrast between fundamental and realized niches. Cajander [38] noted that 'external factors are far from sufficient to explain the occurrence of plants in nature. One crucial factor needs to be included: the war of everything against everything' [40, p. 295]. The use of climate envelope models that only include abiotic descriptors may seem to be at odds with this early insight. However, because these models are purely correlative and fitted to species realized niches, they may describe effects of biotic interactions indirectly via correlated abiotic variables. Still, models including densities or presence/absence of strongly interacting species should be superior. Indeed, several studies have shown that the accuracy of species distribution models is improved by explicitly including biotic factors [8–9,42].

Not only should biotic interactions be included in envelope models, our study shows that it may also be necessary to account for effects of environmental conditions on the strength of biotic interactions. This type of context dependence has been observed in terrestrial, marine and freshwater ecosystems and includes a variety of biotic interactions, from parasitism to competition to mutualism [2,4,43,44]. Climate change will alter a host of environmental conditions both in terms of average conditions and the frequency of extreme events [45,46], and this will, in turn, alter the strength and/or character of many biotic interactions. Thus, it is paramount that the context dependency of species interactions is understood and incorporated in models predicting the effects of climate change on species ranges.

As long as the interacting species are both absent and present along the entire environmental gradient, detecting context dependency using observed species distributions should be possible. However, if the interacting species is only present along one part of the gradient, correlative models will be unable to separate the effects of abiotic and biotic variables. A negative correlation between two species may simply reflect different niche requirements or dispersal abilities. In the latter case, manipulative experiments along environmental gradients will be necessary to elucidate context dependence in species interactions.

Although our model of the coexistence niche of brown trout and pike performed very well, it may be possible to improve future predictions of coexistence under climate change. First, air temperature projections for Sweden should be downscaled from 50 km resolution [47], especially given that coexistence is most threatened in small lakes (less than 1 km²). Second, models that link air temperature to lake thermal dynamics (e.g. duration of summer stratification and winter ice cover, seasonal temperature profiles) [48,49] could be used to improve the characterization of the trout–pike coexistence niche. The strong temperature threshold in the performance of pike feeding on trout [13] suggests that temperature metrics other than mean annual air temperature (e.g. number of days with water temperatures more than 10°C) may better represent the coexistence niche. Third, historic averaged temperature data and fish distribution data did not precisely coincide over time.

In addition, a brown trout distribution model should be developed to predict the full range of climate change impacts on brown trout populations. The direct effects of temperature, the size of inlet and outlet streams for spawning and rearing, lake productivity and the presence of other fish species may also influence how brown trout respond to climate change [17,22,50]. For example, the distribution of brown trout in small, cold, unproductive lakes is limited by competition with Arctic char, but climate change may favour brown trout as lakes become warmer and more productive [50].

In this study, we show that understanding the distribution of brown trout requires that we consider the context dependency of species interactions. Context dependency of species interactions is a general property of ecological systems and has been observed over a wide variety of environmental gradients, including temperature, stream flow, tidal immersion, environmental stress (i.e. elevation) and habitat area [2–4,43]. Because climate change will alter many abiotic conditions in addition to temperature, understanding the environmental context of species interactions is vital for creating useful, future scenarios of species distributions.

5

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