Potential effects of climate change on the distribution of the common frog Rana temporaria at its northern range margin

Lior Blank[a], Miska Luoto[b] & Juha Merilä[a]

[a] Ecological Genetics Research Unit, Department of Biosciences, FI-00014 University of Helsinki, Finland

[b] Department of Geosciences and Geography, FI-00014 University of Helsinki, Finland
Published online: 28 Feb 2014.

PLEASE SCROLL DOWN FOR ARTICLE

Potential effects of climate change on the distribution of the common frog *Rana temporaria* at its northern range margin

Lior Blank[a]*, Miska Luoto[b] and Juha Merilä[a]

[a]Ecological Genetics Research Unit, Department of Biosciences, FI-00014 University of Helsinki, Finland; [b]Department of Geosciences and Geography, FI-00014 University of Helsinki, Finland

Climate change is projected to be particularly strong in northern latitudes, and subarctic species are thus likely to be especially susceptible to the effects of climate warming. We forecast potential effects of climate change on the extent of the suitable habitat of the common frog, *Rana temporaria,* at the margin of its northern range. We investigated 179 potential breeding sites in subarctic Finland and subjected the data to detailed bioclimate envelope modelling using three state-of-the-art techniques: generalized additive models, maximum entropy and generalized boosting methods. Moreover, we included local environmental factors in the models to investigate whether they improve model performance. Under all tested climate change projections and irrespective of the modelling method, the suitable habitat for *R. temporaria* increased in warming climate. The inclusion of local abiotic variables significantly improved the performance of the models. However, June temperature appeared to be the most informative variable in all modelling approaches: a major increase in the extent of suitable habitat occurred when it increased by 1°C. Overall, the modelling results indicate that the distribution of northern *R. temporaria* is likely to be very sensitive to climate warming. The results also highlight the fact that overlooking local abiotic variation can significantly bias bioclimatic modelling results.

Keywords: Alpine amphibian; Arctic; mountain tundra; species distribution modelling

Notes on contributors

Lior Blank is currently an associate researcher at the University of Haifa, Israel. His research interests include spatial and landscape ecology, landscape genetics and species distribution modelling.

Miska Luoto is a professor in the University of Helsinki's Department of Geosciences and Geography. He is interested in biogeography, species distribution modelling and global changes in Arctic–alpine ecosystems.

Juha Merilä is a professor at the University of Helsinki, Finland. His main research interests are evolutionary biology and genetics.

Introduction

Over recent decades, declines and extirpations of amphibian populations have been reported in many parts of the world (Pounds et al. 2006; Wake & Vredenburg 2008; Rohr & Raffel 2010; Duarte et al. 2012). Climate change is among the many hypotheses postulated to explain these declines (Collins & Storfer 2003; Piha et al. 2007; Wake & Vredenburg 2008). In Europe, amphibian species distributions have been forecast to change considerably in the twenty-first century due to climate change. For example, Araújo et al. (2006) modelled the distributions of several European amphibian species in response to five climate change scenarios for 2050. Results of this modelling exercise show that a great proportion of amphibian species are projected to expand their distributions if dispersal is unlimited. This would occur if cooler northern ranges of species become warmer, creating new opportunities for colonization. Being ectothermic ('cold-blooded'), amphibians cannot regulate their body temperature, but instead rely on external heat and behavioural thermoregulation to reach their preferred body temperature (Snyder & Weathers 1975); thus their ability to cope with low temperatures is limited. In fact, most amphibians are unable to persist in areas where average annual temperatures are below 4°C (Snyder & Weathers 1975). An additional effect of rising temperature on amphibians in northern regions is the melting of water bodies that are used for overwintering. Consequently, temperate-zone amphibian species are likely to be more sensitive to climate cooling than warming.

Climate change will have impacts on the life histories, physiologies and geographical distributions of species, possibly resulting in contracting, expanding or shifting community distributions (Hughes 2000; Parmesan et al. 2000; Pöyry et al. 2008). Clearly, these expected and already ongoing changes are of growing concern in a conservation context, because it seems unlikely that the current conservation plans will provide sufficient protection in the future. It is clear that some species have already responded to recent climate change trends by changing their distribution (Warren et al. 2001; Walther et al. 2002; Hickling et al. 2006; Pöyry et al. 2008), phenology (Hughes 2000; Parmesan et al. 2000; Franco et al. 2006), and that community changes have begun (Brown et al. 1997; Hughes 2000; Pounds et al. 2006).

The common frog (*Rana temporaria*) is considered to be a generalist in its habitat use (Van Buskirk & Arioli 2005) and is geographically one of the most widespread anuran amphibians of Eurasia (Gasc et al. 1997). Latitudinally, its distribution range spans from the Pyrenees and northern Greece to the North Cape and the Barents Sea. Longitudinally, it occurs from the Spanish west coast beyond the Ural Mountains in the east. It also inhabits a wide range of altitudes, occurring from sea level up to 2811 metres above sea level in the Italian Alps (Tiberti & von Hardenberg 2012), and up to 1000 m in the Scandinavian mountains (Fog et al. 1997).

*Corresponding author. Email: liorblank@gmail.com

Climatic factors have been shown to affect the distribution of a number of amphibian species (Thomas et al. 2004; Pounds et al. 2006; Broennimann et al. 2007). Thus, it is likely that changing climatic conditions will also alter common frog distribution, and that niche-based models (Guisan & Thuiller 2005) can provide information on the nature and magnitude of these potential shifts. Currently, predictions of how species will respond to climate change are typically based on coarse-grained climate surfaces that utilize bioclimate envelope modelling (Pearson et al. 2004; Huntley et al. 2008). These models represent an approximation of a species' realized niche which is that subset of the fundamental niche that the species actually occupies (Holt 2009). The explained variable for modelling the realized niche-based models is the species location, along with environmental variables such as temperature, precipitation, elevation, etc. The main function of these models is to identify areas that satisfy the requirements of the species' ecological niche (Blank & Blaustein 2012). Although bioclimatic envelope models can provide useful first approximations of the direction and magnitude of the shifts in species' ranges, they have a number of limitations (Pearson & Dawson 2003; Lawler et al. 2006; Luoto & Heikkinen 2008). Predictions may be significantly improved by combining the local abiotic variables into the models (Tingley & Herman 2009; Titeux et al. 2009). This enables the identification of areas with suitable climate but lacking appropriate local environmental conditions (Heikkinen et al. 2007). In addition, niche-based model approaches usually assume that changes in species range are determined mostly by environmental conditions, without additional limitations such as dispersal ability, biotic interactions or life history (Angert et al. 2011; Peterson et al. 2011). Additionally, the *R. temporaria* population we studied resides at the northern edge of the species distribution. This region is one of the coldest locations in continental Europe. Studying marginal populations is important, as theory suggests that shifts in population range at the edge of species' distribution should be one of the first signs of their broad-scale response to environmental changes (Caughley et al. 1988). However, use of niche-based models may be problematic for marginal populations, where the environmental conditions might represent only part of the species' niche (Braunisch et al. 2008). The aim of this study was to explore how climate change is likely to influence the availability of suitable habitat for Arctic–alpine common frogs living at the current margin of their distribution range. To this end, we surveyed 179 potential breeding sites in an area covering a total of 48 km^2 of high-latitude mountain birch forest and alpine heath in north-western Finland. This data was then subjected to detailed bioclimate envelope modelling using three modelling techniques: generalized additive models (GAM), maximum entropy (MAXENT) and generalized boosting method (GBM). In order to investigate whether incorporation of local abiotic factors into the bioclimate envelope models improves the model performance and alters interpretation of the results, we compared climate-only models to climate-environment models.

Methods

The study area

The data for this study were collected from 5 to 17 June 1999 in the vicinity of Lake Kilpisjärvi in north-western Finland (ca 69°03′N, 20°50′E; Figure 1). The snowmelt in Kilpisjärvi starts in late May, and the valleys are usually snow free by mid-June. The snowmelt in fells occurs about a week later. The average June temperature is 7.5 °C (July: 10.9 °C; August: 10 °C). The length of the thermal growth season is about 100 days, whereas the length of thermal summer (> 10 °C) is only c. 40 days (Järvinen 1987). Night temperatures drop regularly below zero as early as September. The number of days with snow cover varies between 185 and 245 (Drebs et al. 2002).

The study area covered a total of 48 km^2 of mountain birch forest and open mountain tundra, as depicted in Figure 1. It can be divided into three main segments (Figure 1; A–C): area 'A' is

a valley (Siilasvuoma) consisting mainly of bogs, ponds and lakes surrounded by mountain birch forest, and to a minor degree (in the eastern part of the area) of open mountain tundra. Area 'B' belongs to the Malla Nature Reserve, whose south and south-western parts consist of a rich mosaic of small bogs and ponds surrounded by flourishing mountain birch forest (Henttonen et al. 1980). The more eastern and northern parts of the area are open mountain tundra. Area 'C' is open mountain tundra (except for the southernmost part, which lies in the mountain birch zone), devoid of vegetation. These areas were selected for the census work to cover a representative range of habitats and altitudes found in the region. However, there were more potential breeding sites at lower altitudes than in higher altitudes (see below).

Census methods

The bogs, ponds and lakes to be surveyed were first identified from topographic maps (1:25,000) and aerial photographic images. These potential breeding sites were visited once, after the egg-laying period in a number of closely monitored breeding sites was over. All potential breeding sites were surveyed for egg masses, which are typically laid in shallow and sun-exposed portions of the water bodies. While it is unlikely that any already laid masses were overlooked, there is always a possibility that some clutches were laid after the localities were censused. However, the bias due to this source of error should be minimal for two reasons. First, close monitoring of two breeding sites in this area over a six-year period has shown that most clutches in a given site are laid within a 2–5-day interval, as the common frog is an explosive breeder (Alho et al. 2008). Second, close monitoring of the two ponds and revisits to a number of additional sites in 1999 did not reveal any newly laid clutches (J. Merilä, unpublished data). As *R. temporaria* females typically lay only one clutch per year (Piha et al. 2007), the number of clutches can be assumed to correspond to local female population size (Johansson et al. 2006; Piha et al. 2007). Nevertheless, inter-annual variability in amphibians breeding might still be a concern (Caldwell et al. 1991). For instance, recruitment failures resulting from breeding failures due to environmental conditions (e.g. droughts or cold summers) or yearly fluctuations in numbers of breeders might lead to yearly variation that would go undetected when sampling is done in one year only. However, most of the sites we sampled are permanent lakes or small ponds that do not dry out even in dry years. Furthermore, meteorological data from Kilpisjärvi region indicate that the conditions in 1999 were similar to the long-term conditions (1952–2012): annual rainfall was 514 mm in 1999 (compared to an annual average of 449 mm) and the average temperature was −1.85 °C (compared to an annual average of −2.19 °C) (Finnish Meteorological Institute). In addition, the ice-free period for Kilpisjärvi Lake was similar to the long-term average (1960–2012): break-up in 1999 was on 17 June (compared to the long-term average of 18 June) and freeze-up in 1999 was on 6 November (compared to the long-term average of 9 November), indicating that the overall climactic conditions in the region were close to the long-term average. In addition, monitoring two breeding sites included in this study has found that the annual number of breeding females remained rather constant over a six-year period (Alho et al. 2008). Furthermore, even if droughts or other kinds of breeding failures (e.g. cold summers, freezing of eggs) occurred, the fact that the females exhibit very high survival rates (Alho et al. 2008) and reach ages up to 18 years (Patrelle et al. 2012) means that yearly fluctuations in numbers of breeders are buffered by a very large number of overlapping generations.

Species distribution modelling (SDM)

SDMs were generated using three different algorithms. These included generalized additive models (GAM), maximum entropy
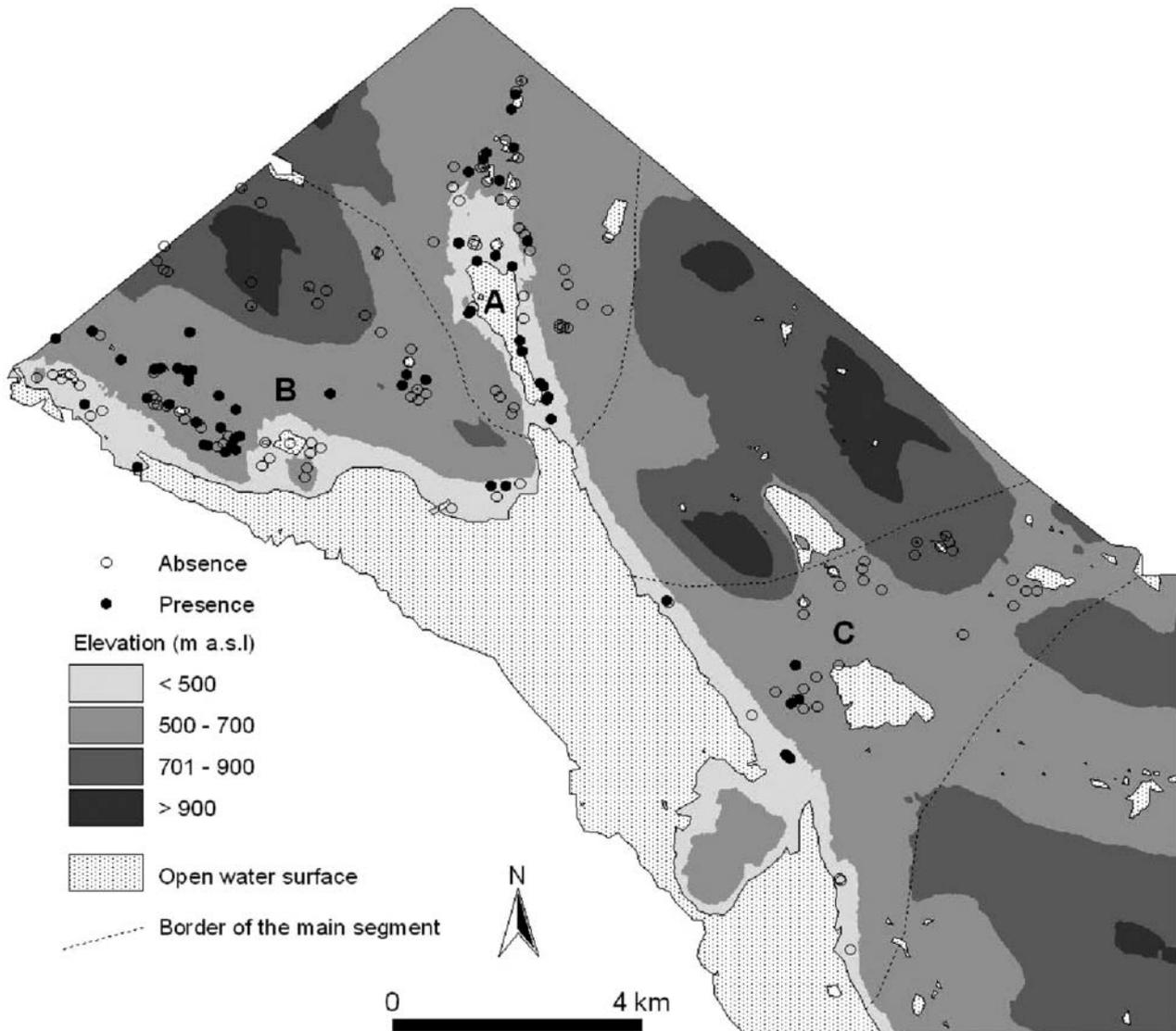
Figure 1.   A map showing the study area, elevation and common frog populatiuons (black dots). Censused but not inhabited localities are shown with open circles. Smaller ponds, bogs and streams have been omitted for ease of interpretation. Three main segments of the study area are indicated by letters A, B and C.

(MAXENT) and generalized boosting method (GBM, also known as boosted regression trees/BRT). Recent studies comparing several techniques of predicting species distribution found that GAM, MAXENT and GBM were among the most effective methods to model species occurrence (Elith et al. 2006; Hernandez et al. 2006; Heikkinen et al. 2012). These three model types have been described in detail by Marmion et al. (2009), Phillips et al. (2006) and Olden et al. (2008), respectively. All of the model types except MAXENT require species presence/absence data for model calibration. MAXENT requires presence-only species data and was applied via the free-release MaxEnt software (version 3.3.3a) (Phillips et al. 2006). GAM and BRT models were run in R programme using mgcv and gbm libraries (R Development Core Team 2010). All models were run with 70% of the training dataset randomly chosen as a test dataset and the remaining 30% used for model validation.

We assessed the predictive performance of the model using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot. AUC provides an assessment of the agreement between the observed records and the model predictions (Fielding & Bell 1997). The AUC values range from 0.5 for models that are no better than random to 1.0 for models with perfect predictive ability (Swets 1988). Thus, an AUC value of 0.8 means the probability is 0.8 that a record selected at random from the set of

presences will have a predicted value greater than a record selected at random from the set of absences.

Explanatory variables

In total, six environmental variables were used to explain common frog occurrence at the resolution of 100×100 m (Table 1). Mean temperature of June was derived from the Finnish

Table 1.   Explanatory variables used in the analysis to determine potential distribution of *R. temporaria*.

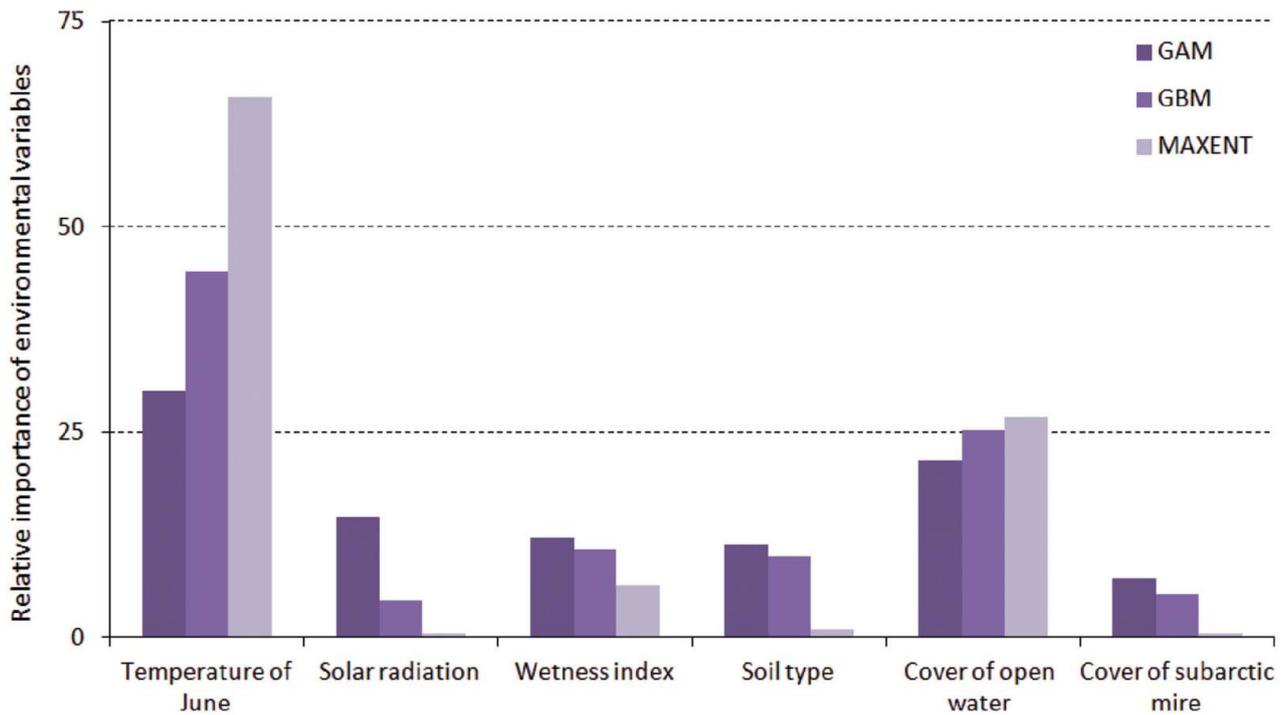| Environmental predictor variables	Units	Mean (min–max)
Radiation	Mj cm^{-2} year^{-1}	0.43 (0.2–0.84)
Soil type	Class	
Topographical wetness	-	7.06 (4.73–11.57)
Water cover	%	4.14 (0–98.92)
Subarctic mire cover	%	5.04 (0–100)
June temperature	°C	6.58 (4.55–7.74)

Figure 2. Relative importance of environmental variables based on GAM, GBM and MAXENT techniques for common frog occurrence.

Meteorological Institute climate data sets (Venäläinen & Heikin-heimo 2002) and averaged for the time period 1971–2000. Temperature data were downscaled from a 30-year data set (1971–2000) from the original 10 km² grid to a 1 ha grid by relating mean June temperature to latitude, longitude and altitude of each study site through multivariate regression (r² of the model: 0.97; for details, see van der Linden & Christensen 2003). The topography variables included mean topographical wetness index (Beven & Kirkby 1979) and mean radiation (Mj cm^{-2} year^{-1}; McCune et al. 2002). These variables were derived from the digital elevation model (DEM) at 25 m resolution using the ArcGIS and ArcView software. The soil type variables, related in the study as percentage covers for each study square, were sand/gravel, moraine, peat and rock. Soil variables were derived from digital maps of Quaternary deposit and pre-Quaternary rocks using ArcGIS software. We also used percentage covers of water and open mire derived from land-cover map. We utilized European land-cover and land-use classification CORINE Land Cover 2000 (Coordination of Information on the Environment) at the resolution of 25 × 25 m as land-cover information in our analysis (European Commission 1994). The spatial data at the resolution of 25 m was converted to 100 m resolution using the ArcGIS software based on the resample function in Spatial Analyst extension.

Climate scenarios

We investigated the temperature sensitivity of common frog occurrence in subarctic NW Finland using all three modelling methods. The June temperature values were modified by one degree in the range of −2 °C and +5 °C. Our sensitivity analysis for June temperature between −2 and +5 matches relatively well with the very recent scenario models (min + 0.8 °C and max + 5.49 °C) for Northern Finland: a 19-model ensemble average for the SRES A1B scenario forecast an increase of 3.54 °C increase, a simulation of the Australian CSIRO-MK3.0 GCM for the SRES B1 scenario forecast an increase of 0.89 °C and a simulation of the Japanese MIROC (medres) GCM for the SRES A2 scenario, which consistently ranks among those simulations giving higher annual temperature and precipitation

increases for Finland, forecast an increase of 5.49 °C (Virkkala et al. 2013).

Precipitation was excluded from the analysis as a result of three lines of reasoning. First, the amount of precipitation does not vary notably within the study area (Sormunen et al. 2011). Second, the projected water balance (annual precipitation–potential evapotranspiration) changes are very minor in the region based on different climate change scenarios (Jylhä et al. 2004). Third, the projected seasonal and annual precipitation changes for northern Finland were generally below or close in magnitude to the natural variability (Jylhä et al. 2004).

Change in the extent of suitable habitat

Next, change (%) in the extent of suitable habitat under different climate change scenarios for the period was investigated. First, the probabilities of species occurrence obtained from the models were transformed into presence and absence by using three different binarization approaches: a cut-off defined by a threshold that 1) maximizes the sum of sensitivity and specificity values (TSS), 2) maximizes the Kappa values and 3) equals sensitivity (true presences) and specificity (true absences; Liu et al. 2013). The transformation to presence and absence was needed when calculating the changes in species distribution. Present and potential future range sizes were estimated from the number of grid cells where species occurred or were predicted to occur. If the current 'potential presence' grid cell was changed to absent (1 to 0), the species was lost. If the current 'potential absence' grid cell was changed to presence (0 to 1), the species increased range size. The species range size remained stable if the species presence or absence did not change (Luoto & Heikkinen 2008).

Results

Current distribution

R. temporaria egg clutches were found in 58 of the 179 potential breeding sites that were surveyed. Frogs were found throughout most of the censused area, but the breeding sites were not evenly
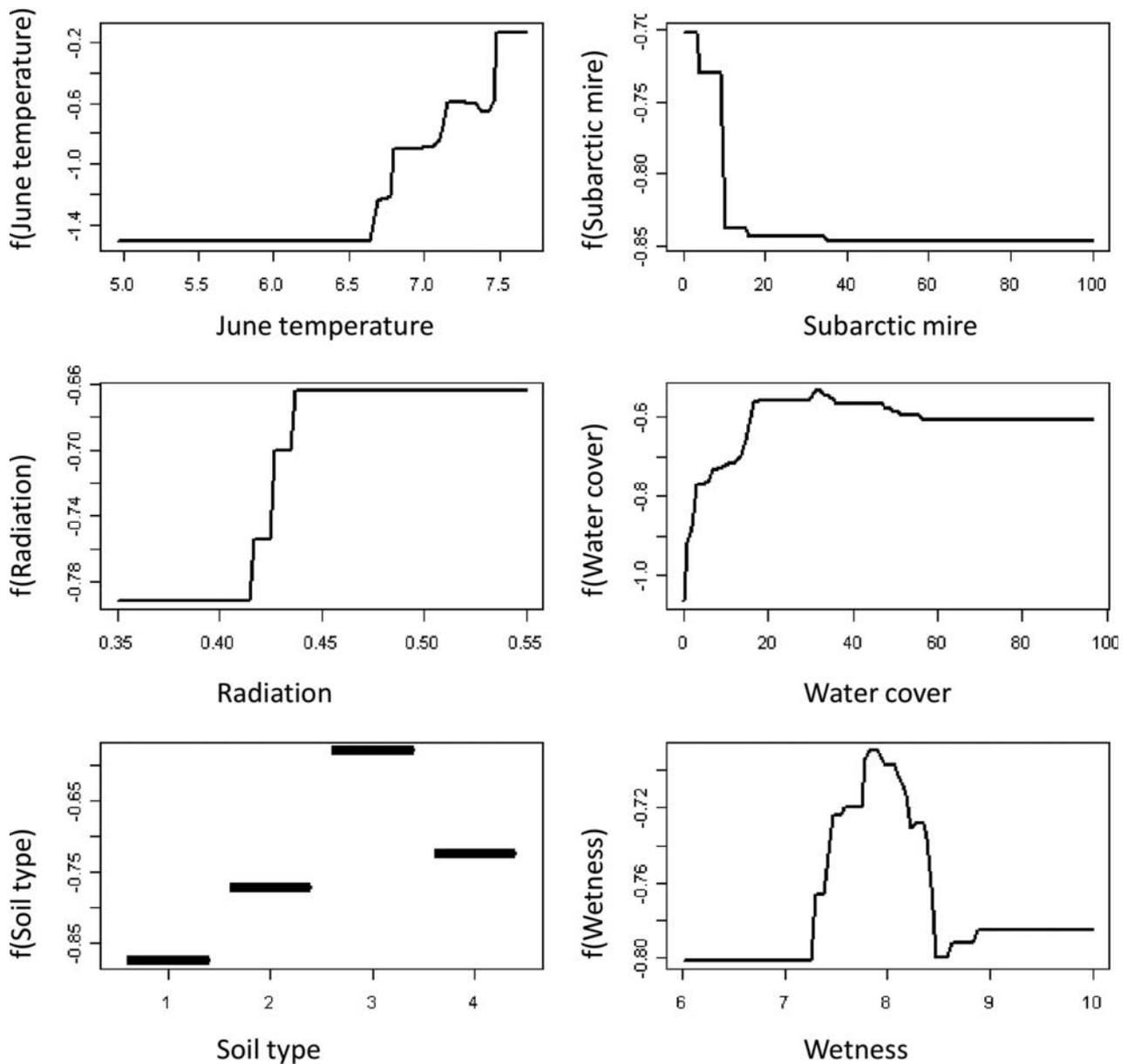
Figure 3.   Response shapes of the environmental variables explaining common frog occurrence based on generalized boosting method (GBM).

distributed (Figure 1). Also, there was a clear tendency for more of the potential sites to be occupied in the neighbourhood of breeding sites with many clutches than in the neighbourhood of breeding sites with few clutches.

The six environmental variables included in the models displayed only weak (Spearman's correlation coefficient, |r| < 0.50) correlations with each other. The environmental variable with the highest contribution – based on all three different modelling techniques – was June temperature, which therefore appears to be the most informative variable to explain species occurrence (Figure 2). The second most important variable was coverage of open water, whereas the contribution of the other four variables varied considerably between the different modelling techniques. The average (mean of the 20 models) AUC values for the climate-only models ranged from 0.66 to 0.71 in the model calibration data and from 0.64 to 0.65 in the model evaluation data, respectively, indicating relatively low performances of the models. The inclusion of abiotic variables significantly increased the AUC values of the models, both in model calibration and evaluation (Wilcoxon signed rank tests, P < 0.001; Table 2), except in the MAXENT model for the evaluation data.

The average AUC values for the climate-environment models ranged from 0.76 to 0.77 in the model calibration and from 0.68 to 0.70 in the evaluation data, respectively.

As an illustrative example, response shapes of the climate and environmental variables that explained common frog occurrence in NW Finland based on the generalized boosting method are presented in Figure 3. Next, we checked three threshold approaches used in order to transform the probabilities of species occurrence (Figure 4). We could see some minor differences in the results based on different binarization methods, but overall the trend was robust.

The modelled current distributions of *R. temporaria* based on climate-only and climate-environmental models using all three different modelling techniques are presented in Figure 5. According to the climate-only models, the species has suitable climate space to occupy, covering 19–23% of the study area. The predicted distribution maps for *R. temporaria* showed a trend of becoming more detailed and patchy as local environmental variables were included. The model also showed an area in a southern region of the study area as being suitable, although this area is yet to be surveyed more extensively.

Table 2. Modelling accuracy mean (minimum–maximum) for the climate-only and climate–environment models measured by the AUC (area under the curve of a receiver operating characteristic plot). The Wilcoxon signed rank tests were used to test the difference between the climate-only vs. climate–environment models based on 20 separate random models. †Statistically significant P-values (p < 0.05) after Bonferroni correction for six comparisons.

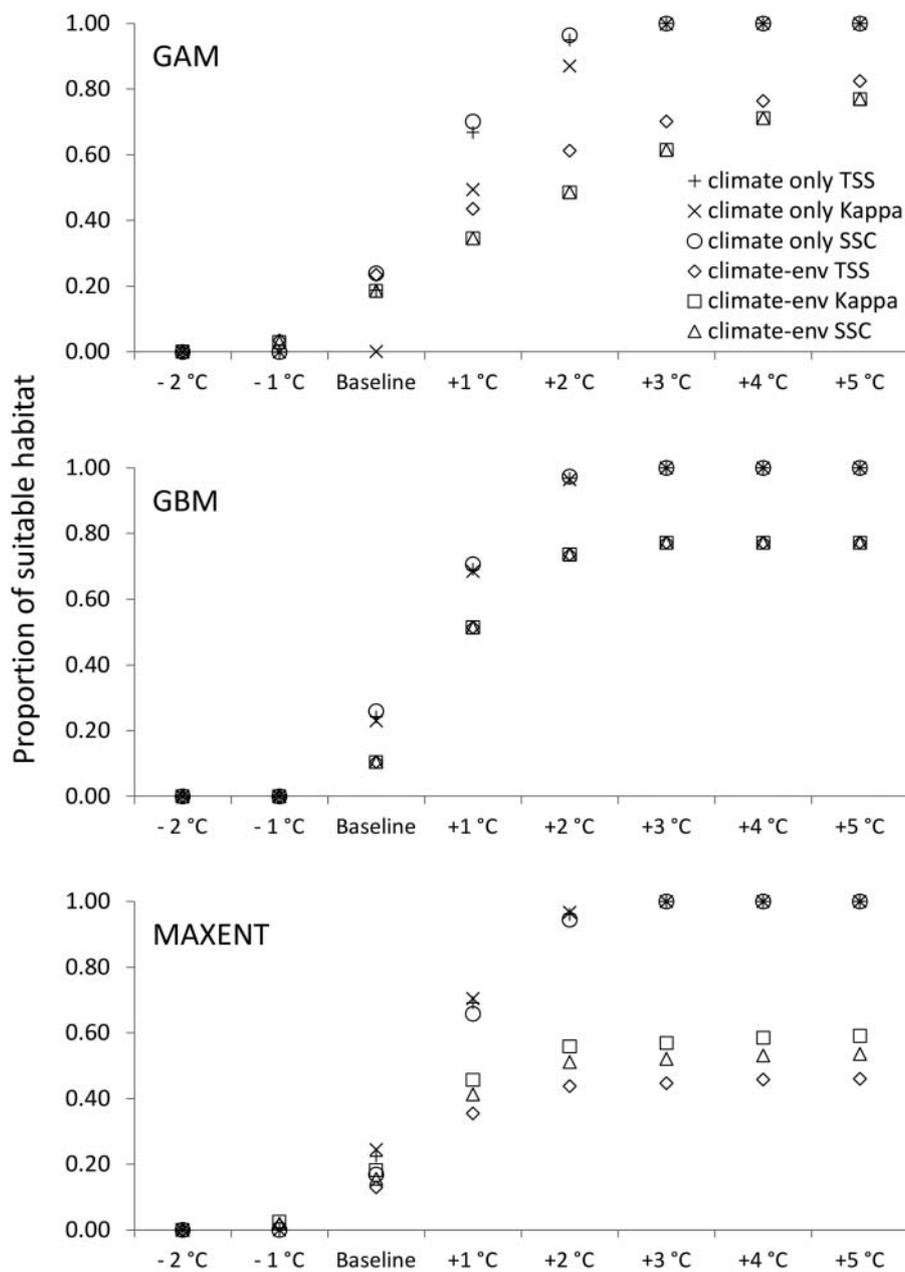|	Climate-only model	Climate–environment model	P-value
GAM model			
AUC calibration	0.68[0.63–0.71]	0.76[0.72–0.80]	<0.0001†
AUC evaluation	0.65[0.51–0.74]	0.70[0.58–0.79]	0.0038†
MAXENT model			
AUC calibration	0.66[0.58–0.71]	0.77[0.76–0.79]	<0.0001†
AUC evaluation	0.64[0.52–0.69]	0.68[0.62–0.85]	0.2455
GBM model			
AUC calibration	0.71[0.68–0.74]	0.77[0.71–0.81]	<0.0001†
AUC evaluation	0.65[0.51–0.74]	0.70[0.58–0.79]	0.0003†

Figure 4. The predicted spatial extent of the common frog using the three modelling techniques and three different thresholds: maximizes the sum of sensitivity and specificity values (TSS), maximizes the Kappa values (Kappa) and equals sensitivity and specificity (SSC).
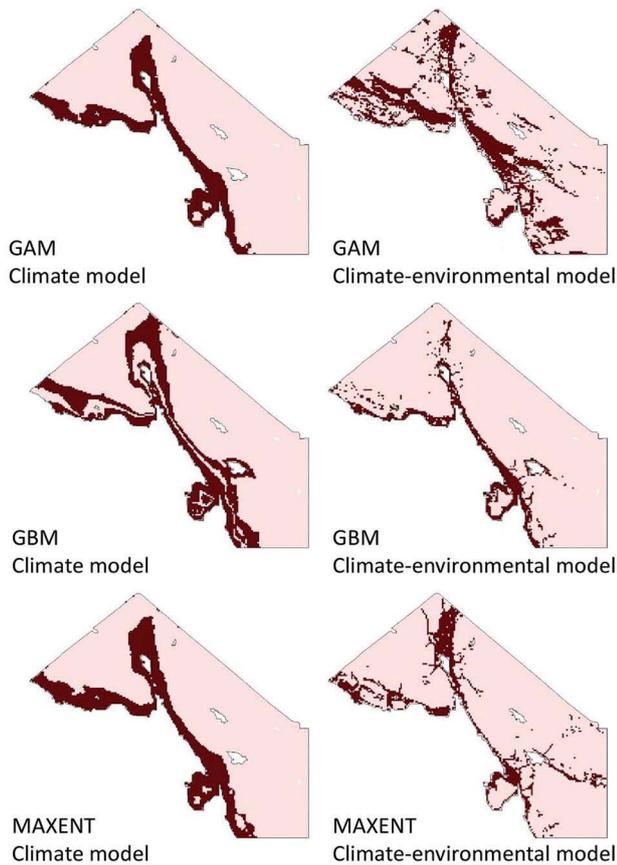
Figure 5. The predicted suitable habitat extent of the common frog using current conditions. We used three different modelling techniques and two sets of predictors (climate-only and climate–environment variables). Dark red represents potential distribution extent using the TSS threshold.

Future distributions of species under climate change

Predicted changes in the extent of suitable habitat relative to observed changes in June temperature, with three different climate-environment models based on climate-only and climate-environment variables, are presented in Figures 6 and 7. Under all tested climate change projections, the suitable habitat for *R. temporaria* increased over time. The major expansion in suitable habitat availability occurred when temperature increased by 1 °C, and the increment in the proportion of occupied cells levelled off after a 2 °C increase (Figure 7). The level of suitable habitat expands mainly along the coast of Lake Kilpisjärvi and smaller lakes (Figure 6). The model predicts that higher elevation habitats characterized by small water bodies, some fluvial activity and relatively sunny slopes will be the most suitable areas for *R. temporaria* colonization in a warming climate (Figure 6), whereas the homogeneous mountain tundra above 800 m showed relatively low probability values in all projections.

Discussion

The results of this study – based on empirically validated models – show that the extent of suitable habitat for *R. temporaria* on the northern margin of its range is expected to increase considerably in a warming climate, reflecting a broad magnitude of climate impact rather than fine-scale effect (Pearson & Dawson 2003). The results were relatively consistent among different models and should give fairly good insight into the overall patterns of potential future distribution. As inherent to all similar modelling exercises, the predictions are conditional on compounded uncertainty

in climate change scenarios (IPCC 2007), as well as the lack of inclusion of biotic interactions, adaptation potential or dispersal ability (Pearson & Dawson 2003; Dormann 2007; Heikkinen et al. 2007). In fact, there is contradictory evidence showing that while the distribution of many species coincides with models' predictions, for others it does not (Tingley & Herman 2009; Lenoir et al. 2010). Thus, niche-based models should not be interpreted as predicting actual range of species, but rather used to identify regions characterized by similar environmental conditions in which the species is known to occur (Pearson et al. 2007). Despite these inherent uncertainties, the models can be used as a framework to support conservation planning and to provide a first step to understanding the possible effects of rapid climate change (Guisan & Thuiller 2005).

Another potential problem may arise when projecting the models on to different climate scenarios while only modelling part of the species range. Incomplete coverage of projected future climates can produce prediction errors. For example, in our study, southernmost and/or lowest regions are projected to experience a future climate that has no modern analogue in the study region. In such cases modelling results might provide incomplete information of how species might respond to non-analogue situations (see e.g. Heikkinen et al. 2006). This may lead to projections of species loss in the warmest parts of the study area being an artifact. However, in our study, common frog response to the June temperature showed a constant positive trend irrespective of the statistical technique implemented. Thus, we do not see that this issue will have a strong effect in the modelling outputs. In addition, we think that projecting the results on to a wider geographical range would be problematic when considering the fact that *R. temporaria* shows a high degree of local adaptation and genetic heterogeneity over even very short distances (Laugen et al. 2003; Palo et al. 2003; Palo et al. 2004). Hence, we think the results should not be generalized to cover the entire distribution range of this species, but rather be specific to the geographic area (or its proximity) covered here.

Although bioclimatic envelope models can provide useful first approximations of the direction and magnitude of species range shifts, they have a number of limitations (Pearson & Dawson 2003; Heikkinen et al. 2006; Lawler et al. 2006; Luoto et al. 2007). In this study we address two of these potential limitations. First, an increasing body of evidence suggests that the projections of species distributions derived from bioclimatic envelope models may vary considerably depending on the modelling technique applied (Heikkinen et al. 2006). Consequently, it is now commonly considered that evaluation of climate change's potential impacts on species ranges should be based on outputs from more than one modelling technique (Araújo & New 2007; Marmion et al. 2009). In this study, the results from the different modelling techniques were in good agreement, increasing confidence in the predictions made. Second, in contrast to the impacts of modelling techniques, the consequences of disregarding local environmental conditions (in essence, topographical and soil heterogeneity) for the outcomes of bioclimatic envelope models have been investigated only rarely (but see Peterson 2003; Luoto & Heikkinen 2008; Ashcroft et al. 2009).

The expected response to climate change depends on whether the predictions are based on climate-only or climate–environment models. One reason why the suitable habitat maps of the latter are more fragmented than the former relates to the possibility of unsuitable soil type. Although the observed effects varied between the modelling techniques, some clear trends could still be distinguished. In general, projections of range size changes of *R. temporaria* derived from climate-only models appear more pronounced than projections based on climate–environment models; hence, the climate-only models are likely to overestimate the expected responses, and therefore be overly liberal. Hence, the results generate questions about the appropriateness of making forecasts of species range size changes at the local scale without taking into account relevant environment variables. Disregarding local factors in species distribution models

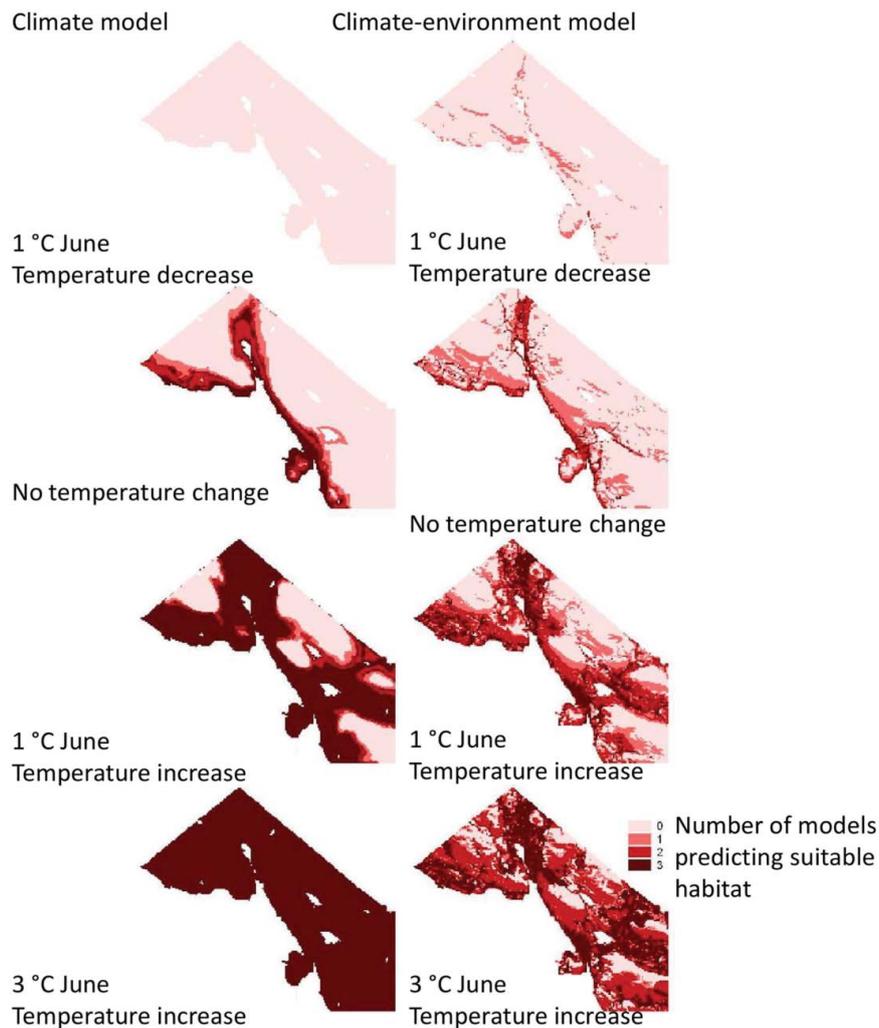Climate model   Climate-environment model

Figure 6. The predicted suitable habitat extent of the common frog using different June temperatures and using the TSS threshold. We used three different modelling techniques and two sets of predictors (climate-only and climate–environment variables). Note that the number of models to predict the species' suitable habitat is illustrated by different colour symbols.

may result in biased projections of range expansions and the associated colonization, extinction and turnover assessments (Luoto & Heikkinen 2008).

Apart from the methodological implications, these results also have a more fundamental message: they support the conjecture that climate is one of the main determinants of *R. temporaria* distribution. This is not to say that local environment would not have an important role in determining *R. temporaria* occurrence. Indeed, the inclusion of local environmental variables changed the present and forecast future distribution of *R. temporaria*. This is not surprising given that earlier autecological studies of this species have found that the proximity of suitable summer habitat – moist grassy meadows – is an important predictor of the species' absence or presence from a given potential breeding site (Loman 1988). Furthermore, as the species in our study site overwinters in water, in streams, springs or lakes which do not freeze to the bottom, the importance of local environmental conditions as reflected in soil and topographic parameters is understood. Topography controls the winter-time freezing of the aquatic habitats through the snow accumulation, i.e. the depth of freezing is inversely proportional to the depth of snow. Moreover, topography determines the amount of solar radiation and temperature, and the moisture conditions of the soil at the local habitats. These conditions affect, for example, vegetation type and spatial pattern (Li et al. 2010) and water temperature at the breeding sites, which in turn affect abiotic parameters such as dissolved oxygen (Skelly et al. 2002). In addition, soil was found to influence the distribution of

many amphibian species (Diller & Wallace 1999; Bradford et al. 2003; Dayton et al. 2004; Blank & Blaustein 2012). Different soil types have, for example, distinct water-holding capacity (Schiller et al. 2010) and were found to support different plant communities (Kruckeberg 2004; Wijesinghe et al. 2005). The combined inclusion of topography and soil data in the models makes it possible to identify areas with suitable climatic conditions but unsuitable combinations of topography and soil types (Titeux et al. 2009; Sormunen et al. 2011). These combined effects of topography and soil potentially affect the breeding site selection, and stress the importance of integrating them into climate change impact models.

The importance of local microclimatic conditions for distribution of *R. temporaria* in the study area is also reflected in several observations regarding their breeding biology. First, given the short growth season in the north, the thermal properties of the breeding site are likely to be critical to successful reproduction. For instance, in cold summers and in cool breeding sites subject to influx of cold snowmelt water from fells, the tadpoles frequently fail to metamorphose before the ponds freeze over (Alho et al. 2008). As the Fennoscandian common frogs cannot overwinter as tadpoles (J. Merilä, personal observation), reproduction in cool ponds fails. Hence, the impact of microclimatic factors determining the thermal environment in breeding sites is likely to be an important factor controlling breeding site distribution. This is also seen in the tendency for common frogs in the study area to lay their eggs on the warmest, most sun-exposed sides of water bodies (J. Merilä, unpublished data). The
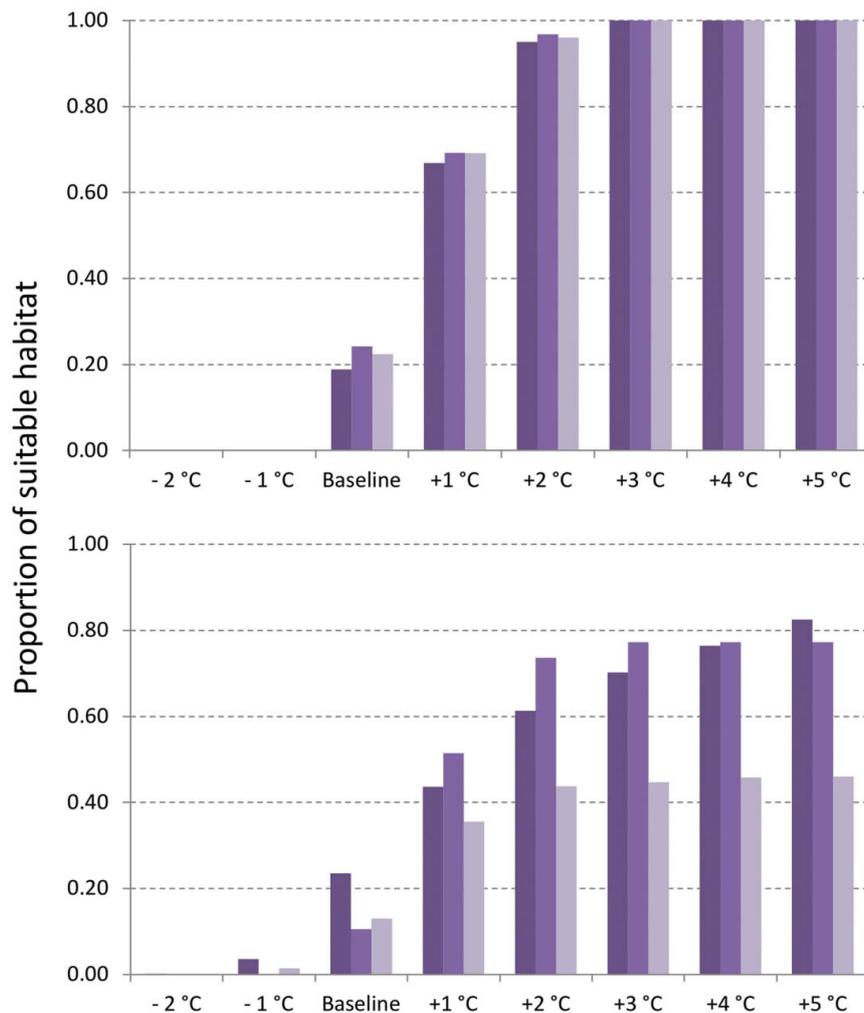
Figure 7. Predicted changes in the extent of suitable habitat relative to observations for changes in June temperature using the TSS threshold. We used three different climate-only models (upper figure) and three different climate-environment models (lower figure) based on GAM (dark blue/grey), GBM (blue/grey) and MAXENT (light blue/grey) modelling techniques.

constraining role of the thermal environment is also reflected in the mating and egg-laying behaviour of the frogs in the study area: in contrast to nocturnal mating and breeding at lower latitudes, common frogs in Kilpisjärvi mate and lay their eggs diurnally when the ambient temperatures peak (J. Merilä, unpublished results). There is also evidence from laboratory experiments to suggest that tadpoles from the study area have a genetic capacity for faster development than tadpoles from lower latitudes (Laugen et al. 2003), giving further support to the conjecture that the low ambient temperatures are a growth-limiting factor in the north.

Conclusions

Taken together, our results indicate that the distribution of *R. temporaria* in northern Fennoscandia is likely to be very sensitive to climate warming. Three different statistical models predicted that warming summer temperatures are likely to significantly increase the suitable breeding area such that an increase of 4 °C in June would result in a three to five-fold increase of *R. temporaria* distribution range. Incorporation of more detailed information into the statistical distribution models could further reduce uncertainty in model estimates. This additional information could be, for example, even more fine-scaled data on other relevant environmental and climatic parameters not included in this study. In particular, accurate information about snow cover, as well as soil and water temperatures, could

improve the model predictions. While the inclusion of more detailed information would likely to further reduce the predicted occupancy area, the fact remains that the predicted impact of climate warming would still be considerable, as illustrated by the results of this study.

References

Alho J, Herczeg G, Merilä J. 2008. Female-biased sex ratios in subarctic common frogs. J. Zool. 275:57–63.
Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011. Do species' traits predict recent shifts at expanding range edges? Ecol. Lett. 14:677–689.

Araújo MB, New M. 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22:42–47.

Araújo MB, Thuiller W, Pearson RG. 2006. Climate warming and the decline of amphibians and reptiles in Europe. J. Biogeogr. 33:1712–1728.

Ashcroft MB, Chisholm LA, French KO. 2009. Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. Global Change Biol. 15:656–667.

Beven KJ, Kirkby MJ. 1979. A physically based, variable contributing area model of basin hydrology/Un modèle à base physique de zone d'appel variable de l'hydrologie du bassin versant. Hydrolog. Sci. J. 24:43–69.

Blank L, Blaustein L. 2012. Using ecological niche modeling to predict the distributions of two endangered amphibian species in aquatic breeding site. Hydrobiologia. 693:157–167.

Bradford DF, Neale AC, Nash MS, Sada DW, Jaeger JR. 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. Ecology. 84: 1012–1023.

Braunisch V, Bollmann K, Graf RF, Hirzel AH. 2008. Living on the edge- modelling habitat suitability for species at the edge of their fundamental niche. Ecol. Model. 214:153–167.

Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson A, Guisan A. 2007. Evidence of climatic niche shift during biological invasion. Ecol. Lett. 10:701–709.

Brown JH, Valone TJ, Curtin CG. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proc Nat Acad USA. 94:9729–9733.

Caldwell I, Vittt LJ, Gibbons JW. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science. 253:892–895.

Caughley G, Grice D, Barker R, Brown B. 1988. The edge of the range. J. Anim. Ecol. 57:771–785.

Collins JP, Storfer A. 2003. Global amphibian declines: sorting the hypotheses. Divers. Distrib. 9:89–98.

Dayton GH, Jung RE, Droege S. 2004. Large-scale habitat associations of four desert anurans in Big Bend National Park, Texas. J. Herpetol. 38:619–627.

Diller LV, Wallace RL. 1999. Distribution and habitat of *Ascaphus truei* in streams on managed, young growth forests in north coastal California. J. Herpetol. 33:71–79.

Dormann CF. 2007. Promising the future? Global change projections of species distributions. Basic Appl. Ecol. 8:387–397.

Drebs A, Nordlund A, Karlsson P, Helminen J, Rissanen P. 2002. Climatological statistics of Finland 1971–2000. Helsinki: Finnish Meteorological Institute; p. 99.

Duarte H, Tejedo M, Katzenberger M, Marangoni F, Baldo D, Beltrán JF, Martí DA, Richter-Boix A, Gonzalez-Voyer A. 2012. Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. Global Change Biol. 18:412–421.

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography. 29:129–151.

European Commission. 1994. CORINE Land Cover. Technical Guide. EUR12585 Luxembourg, Office for Official Publications of the European Communities.

Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24:38–49.

Fog K, Schmedes A, Rosenørn-de Lasson D. 1997. Nordens padder og krybdyr. Copenhagen: G. E. C. Gads Forlag.

Franco A, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B, Thomas CD. 2006. Impacts of climate warming and habitat loss on extinctions at species' low latitude range boundaries. Global Change Biol. 12:1545–1553.

Gasc JP, Cabela A, Crnobrnja-Isailovic J, Dolmen D, Grossenbacher K, Haffner P, Lescure J, Martens H, Martinez Rica JP, Maurin H, et al. 1997. Atlas of amphibians and reptiles in Europe. Paris: Societas Europaea Herpetologica & Museum National d'Histoire Naturelle.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8:993–1009.

Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography. 30:751–777.

Heikkinen RK, Luoto M, Virkkala R, Pearson RG, Körber JH. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecol. Biogeogr. 16:754–763.

Heikkinen RK, Marmion M, Luoto M. 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? Ecography. 35:276–288.

Henttonen H, Järvinen A, Laine K. 1980. Plants, birds and mammals in the Malla nature reserve. Kilpisjärvi Notes 3:1–14.

Hernandez PA, Graham CH, Master LL, Albert DL. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography. 29:773–785.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biol. 12:450–455.

Holt RD. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proc Nat Acad USA. 106:19659–19665.

Hughes L. 2000. Biological consequences of global warming: is the signal already apparent? Trends Ecol. Evol. 15:56–61.

Huntley B, Collingham YC, Willis SG, Green RE. 2008. Potential impacts of climatic change on European breeding birds. PLoS One. 3:e1439.

IPCC. 2007. Summary for policymakers. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ and Hanson CE, editors. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. pp. 7–22. Cambridge University Press: Cambridge, UK.

Järvinen A. 1987. Basic climatological data on Kilpisjärvi area, NW Finnish Lapland. Kilpisjärvi Notes. 10:1–16.

Johansson M, Primmer CR, Merilä J. 2006. History vs. current demography: explaining the genetic population structure of the common frog (*Rana temporaria*). Mol. Ecol. 15:975–983.

Jylhä K, Tuomenvirta H, Ruosteenoja K. 2004. Climate change projections for Finland during the 21 st century. Boreal Environ. Res. 9:127–152.

Kruckeberg AR. 2004. Geology and plant life: the effects of landforms and rock types on plants. University of Washington Press: Seattle, Washington, USA.

Laugen AT, Laurila A, Räsänen K, Merilä J. 2003. Latitudinal countergradient variation in the common frog (*Rana temporaria*) development rates-evidence for local adaptation. J. Evol. Biol. 16:996–1005.

Lawler JJ, White D, Neilson RP, Blaustein AR. 2006. Predicting climate-induced range shifts: model differences and model reliability. Global Change Biol. 12:1568–1584.

Lenoir J, Gégout JC, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Svenning JC. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography. 33:295–303.

Li FR, Peng SL, Chen BM, Hou YP. 2010. A meta-analysis of the responses of woody and herbaceous plants to elevated ultraviolet-B radiation. Acta Oecol. 36:1–9.

Liu C, White M, Newell G. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. J. Biogeogr. 40:778–789.

Loman J. 1988. Breeding by *Rana temporaria*; the importance of pond size and isolation. Memoranda Societatis pro Fauna et Flora Fennica. 64:113–115.

Luoto M, Heikkinen R. 2008. Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. Global Change Biol. 14:483–494.

Luoto M, Virkkala R, Heikkinen RK. 2007. The role of land cover in bioclimatic models depends on spatial resolution. Global Ecol. Biogeogr. 16:34–42.

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W. 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15:59–69.

McCune B, Keon D, Marrs R. 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13:603–606.

Olden JD, Lawler JJ, Poff NLR. 2008. Machine learning methods without tears: a primer for ecologists. Q Rev Biol. 83:171–193.

Palo J, O'Hara RB, Laugen AT, Laurila A, Primmer CR, Merilä J. 2003. Latitudinal divergence of common frog (*Rana temporaria*) life history traits by natural selection: evidence from a comparison of molecular and quantitative genetic data. Mol. Ecol. 12:1963–1978.

Palo JU, Schmeller DS, Laurila A, Primmer CR, Kuzmin SL, Merilä J. 2004. High degree of population subdivision in a widespread amphibian. Mol. Ecol. 13:2631–2644.

Parmesan C, Root TL, Willig MR. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin-American Meteorological Society. 81:443–450.

Patrelle C, Hjernquist MB, Laurila A, Söderman F, Merilä J. 2012. Sex differences in age structure, growth rate and body size of common frogs Rana temporaria in the subarctic. Polar Biol. 35:1505–1513.

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12:361–371.

Pearson RG, Dawson TP, Liu C. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography. 27:285–298.

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34:102–117.

Peterson AT. 2003. Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. Global Change Biol. 9:647–655.

Peterson AT, Soberon J, Pearson RG, Martinez-Meyer E, Nakamura M, Araújo MB. 2011. Ecological niches and geographic distributions. Princeton, NJ: Princeton University Press.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190:231–259.

Piha H, Luoto M, Piha M, Merilä J. 2007. Anuran abundance and persistence in agricultural landscapes during a climatic extreme. Global Change Biol. 13:300–311.

Pounds JA, Bustamante MR, Coloma LA, Consuegra JA, Fogden MPL, Foster PN, La Marca E, Masters KL, Merino-Viteri A, Puschendorf R, et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature. 439:161–167.

Pöyry J, Luoto M, Heikkinen RK, Saarinen K. 2008. Species traits are associated with the quality of bioclimatic models. Global Ecol. Biogeogr. 17:403–414.

Rohr JR, Raffel TR. 2010. Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. Proc Nat Acad USA 107:8269–8274.

Schiller G, Ungar ED, Cohen S, Herr N. 2010. Water use by Tabor and Kermes oaks growing in their respective habitats in the Lower Galilee region of Israel. For. Ecol. Manage. 259:1018–1024.

Skelly DK, Freidenburg LK, Kiesecker JM. 2002. Forest canopy and the performance of larval amphibians. Ecology 83:983–992.

Snyder GK, Weathers WW. 1975. Temperature adaptations in amphibians. Am. Nat. 109:93–101.

Sormunen H, Virtanen R, Luoto M. 2011. Inclusion of local environmental conditions alters high-latitude vegetation change predictions based on bioclimatic models. Polar Biol. 34:883–897.

Swets JA. 1988. Measuring the accuracy of diagnostic systems. Science. 240:1285–1293.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, De Siqueira MF, Grainger A, Hannah L, et al. 2004. Extinction risk from climate change. Nature. 427:145–148.

Tiberti R, von Hardenberg A. 2012. Impact of introduced fish on Common frog (*Rana temporaria*) close to its altitudinal limit in alpine lakes. Amphibia-Reptilia. 33:303–307.

Tingley R, Herman T. 2009. Land-cover data improve bioclimatic models for anurans and turtles at a regional scale. J. Biogeogr. 36:1656–1672.

Titeux N, Maes D, Marmion M, Luoto M, Heikkinen RK. 2009. Inclusion of soil data improves the performance of bioclimatic envelope models for insect species distributions in temperate Europe. J. Biogeogr. 36:1459–1473.

Van Buskirk J, Arioli M. 2005. Habitat specialization and adaptive phenotypic divergence of anuran populations. J. Evol. Biol. 18:596–608.

van der Linden S, Christensen JH. 2003. Improved hydrological modeling for remote regions using a combination of observed and simulated precipitation data. J. Geophys. Res. 108:4072–4083.

Venäläinen A, Heikinheimo M. 2002. Meteorological data for agricultural applications. Physics and Chemistry of the Earth 27:1045–1050.

Virkkala R, Heikkinen RK, Fronzek S, Leikola N. 2013. Climate Change, Northern Birds of Conservation Concern and Matching the Hotspots of Habitat Suitability with the Reserve Network. PloS One 8:e63376.

Wake DB, Vredenburg VT. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proc Nat Acad USA. 105:11466–11473.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. Nature. 416:389–395.

Warren M, Hill J, Asher T, Fox R, Huntley B, Roy D, Telfer M, Jeffcoate S, Harding P, Jeffcoate G, et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature. 414:65–69.

Wijesinghe DK, John EA, Hutchings MJ. 2005. Does pattern of soil resource heterogeneity determine plant community structure? An experimental investigation. J. Ecol. 93:99–112.