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Probabilistic accounting of uncertainty in forecasts of species distributions under climate change

Running head: species distribution uncertainty

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This is a **primary research article**.

Abstract

Forecasts of species distributions under future climates are inherently uncertain, but there have been few attempts to describe this uncertainty comprehensively in a probabilistic manner. We developed a Monte Carlo approach that accounts for uncertainty within generalized linear regression models (parameter uncertainty and residual error), uncertainty among competing models (model uncertainty), and uncertainty in future climate conditions (climate uncertainty) to produce site-specific frequency distributions of occurrence probabilities across a species' range. We illustrated the method by forecasting suitable habitat for bull trout (*Salvelinus confluentus*) in the Interior Columbia River Basin, USA, under recent and projected 2040s and 2080s climate conditions. The 95% interval of total suitable habitat under recent conditions was estimated at 30.1 to 42.5 thousand km; this was predicted to decline to 0.5 to 7.9 thousand km by the 2080s. Projections for the 2080s showed that the great majority of stream segments would be unsuitable with high certainty, regardless of the climate dataset or bull trout model employed. The largest contributor to uncertainty in total suitable habitat was climate uncertainty, followed by parameter uncertainty and model uncertainty. Our approach makes it possible to calculate a full distribution

of possible outcomes for a species, and permits ready graphical display of uncertainty for individual locations and of total habitat.

Introduction

Climate change is expected to alter the distributions of many organisms over the next century, and there have been numerous attempts to forecast these shifts using species distribution models (SDMs; Elith & Leathwick, 2009). Such predictions are fraught with uncertainty from multiple sources: species occurrence records are limited, factors driving species occurrences are known imperfectly, data for important predictor variables may be unavailable, different models yield different predictions, species-environment relationships are plastic, correlations among predictor variables can shift, and scenarios of future climate conditions depend on emissions assumptions, climate model and specified initial conditions (Barry & Elith, 2006, Buisson *et al.*, 2010, Deser *et al.*, 2012, Diniz-Filho *et al.*, 2009, Dormann *et al.*, 2008a, Fronzek *et al.*, 2010, Pearson *et al.*, 2006). Accounting for this uncertainty is critical for effective conservation planning. Locations where extirpation is predicted with high certainty will tend to be low priorities for conservation investments; in contrast, locations with substantial uncertainty in future occurrence probability still have potential and may be especially important locations for monitoring and restoration activities.

A promising approach for dealing with this uncertainty is the use of ensemble forecasting (Araújo & New, 2007). This is a form of multimodel inference or model averaging (Burnham & Anderson, 2002, Dormann *et al.*, 2008b, Hoeting *et al.*, 1999) in which many predictions are made using different models, datasets, or future climate conditions, and then combined. Ensemble species forecasting is analogous to ensemble forecasting of climates (Stainforth *et al.*, 2005). There have been numerous efforts to use ensemble methods to quantify components of uncertainty in species-climate modeling. Studies have examined uncertainty due to modeling method (Bagchi *et al.*, 2013, Diniz-Filho *et al.*, 2009, Dormann *et al.*, 2008a, Pearson *et al.*, 2006, Roura-Pascual *et al.*, 2009), different combinations of predictor variables (Dormann *et al.*, 2008b, Synes & Osborne, 2011), and different climate forecasts (Bagchi *et al.*, 2013, Buisson *et al.*, 2010, Diniz-Filho *et al.*, 2009, Fronzek *et al.*, 2010). However, we know of no study that has used probabilistic ensemble forecasting of species distributions integrating all of these uncertainty sources. Such an approach would combine multiple predictions to generate site-specific distributions of occurrence probabilities that account for uncertainty within models, among competing models, and among different future climate scenarios. Hartley et al. (2006) and Roura-Pascual et al. (2009) used probabilistic methods to forecast suitable habitat for the invasive Argentine ant (*Linepathema humile*), but did not consider climate change and did not fully account for within-model uncertainty. Fronzek *et al.* (2010) used a probabilistic approach to predict global change impacts on the distribution of palsa mires (boreal peat mounds), but only considered climate uncertainty. Araújo and New (2007) called probabilistic forecasting the "end game of ensemble forecasting," and we believe that it is the most comprehensive and accurate way to account for uncertainty.

In this article we describe methods for probabilistic ensemble modeling of future species distributions. We use Monte Carlo methods to sample the range of possible parameters within each of several competing models, weighted according to their degree of support, and use these to make predictions under different future climate scenarios. The many predictions are combined to create distributions of occurrence probability (which we interpret as habitat suitability, since predictions may be made at sites not accessible to the organism) at locations of interest. These may then be summed to produce a histogram of total suitable habitat predictions. We illustrate the methods using bull trout (*Salvelinus confluentus*), a climate-sensitive fish species of conservation interest, in Idaho and western Montana, USA. Past studies have suggested that substantial declines in suitable habitat for bull trout are likely under future climate conditions (Isaak *et al.*, 2010, Jones *et al.*, 2013, Rieman *et al.*, 2007, Wenger *et al.*, 2011). Our main objective is to assess the likelihood of a major versus minor decline by generating a set of probabilistic estimates of total suitable habitat using future climate scenarios. We are also interested in examining the geographic distribution of uncertainty, identifying which components (e.g., model uncertainty, climate uncertainty) contribute the most to total uncertainty in the predictions, and exploring how results can be used to improve species conservation efforts.

Materials and methods

Study species, location and dataset

The bull trout is a salmonid native to western Canada and northwestern U.S., where it is listed as federally threatened under the U.S. Endangered Species Act. It requires very cold streams for spawning and rearing, and has one of the narrowest temperature niches of salmonid species in North America (Dunham *et al.*, 2003, McMahon *et al.*, 2007, Selong *et al.*, 2001). Suitable bull trout spawning habitat occurs primarily in high-elevation streams, limiting the species' potential to migrate to higher-elevation refugia (Isaak *et al.*, 2010, Rieman & McIntyre, 1995), and making its response to climate change of considerable management interest (Lawler *et al.*, 2008, Rieman *et al.*, 2007). We focused the study on the distribution of bull trout in a portion of its range in the interior Columbia River basin (Fig. 1).

Our bull trout dataset consisted of fish collection records at 995 sites. The collections were originally made by state and federal agencies (see *Acknowledgments*) using electrofishing and snorkeling between 1985 and 2004, with most collections made in the late 1990s. Fish data were matched with geomorphic, biotic, and climate variables hypothesized to regulate bull trout distributions. These are fully described in Wenger *et al.* (2011), so we give only a summary here. Geomorphic variables included (1) stream slope (abbreviated as "slope"), which was calculated from digital elevation models, and (2) distance to the nearest unconfined valley bottom ("valleybottom"), a montane landscape feature associated with occurrence of some trout species (Baxter & Hauer, 2000, Benjamin *et al.*, 2007, Cavallo, 1997). The presence of non-native brook trout ("brooktrout", *Salvelinus fontinalis)* at the subwatershed scale (defined by 12-digit hydrologic unit codes or HUCs) was included as a biotic variable because brook trout may have adverse impacts on bull trout (DeHaan *et al.*, 2010, Rieman *et al.*, 2006). Climate variables included (1) mean summer air temperature in the upstream drainage ("temp"); (2) mean summer flow ("baseflow"), which was also an indicator of stream size; and (3) frequency of high flows during winter ("winterflow"), a variable shown to be negatively correlated with the occurrence of fall-spawning fish species such as bull trout (Fausch, 2008, Latterell *et al.*, 1998, Seegrist & Gard, 1972). For model fitting, air temperature data were extrapolated from weather station observations into gridded fields (Hamlet & Lettenmaier, 2005), from which we calculated mean air temperature in the watershed upstream of each site (Wenger *et al.*, 2011). Flow metrics were estimated using the Variable Infiltration Capacity (VIC) macroscale hydrologic model (Liang *et al.*, 1994, Liang *et al.*, 1996) run for the Pacific Northwest at a scale of 1/16th degree (Elsner *et al.*, 2010) and downscaled (Wenger *et al.*, 2010) to stream segments of the 1:100,000 scale National Hydrography Dataset plus (NHDplus; *www.horizon-systems.com/nhdplus*). Climate data used for forecasts were derived from IPCC scenarios (IPCC, 2007) and VIC modeling (Elsner *et al.*, 2010) and are described below under “Prediction uncertainty.”

Modeling method

As the basis for these methods we used generalized linear mixed models (GLMMs) in preference to less restrictive approaches such as regression trees, neural networks, or maximum entropy. Although comparisons have shown that these methods can produce models with very good fits to individual datasets (Elith *et al.*, 2006), such models often lack generality (Heikkinen *et al.*, 2012, Wenger & Olden, 2012), which reduced our confidence in their transferability to novel climatic conditions. GLMMs and their simpler variants, generalized linear models (GLMs), are often comparable to other methods in predictive performance (Dormann *et al.*, 2008a). Moreover, they permit the clear specification of alternative models based on prior ecological knowledge and are supported by well-developed theory for constructing prediction intervals, which we use as the basis for creating probabilistic ensemble prediction distributions.

We used two-level logistic regression models with a random intercept for subwatershed to predict bull trout occurrence as a function of the variables described above. We used mixed modeling because our sites were non-randomly distributed (Wenger *et al.*, 2011), resulting in spatial autocorrelation that could bias parameter estimates (Raudenbush & Bryk, 2002). A random effect allows for the possibility that sites within a subwatershed are not independent from one another (Bolker *et al.*, 2009), reducing bias. Our models differed only in terms of fixed effects.

Model selection and weighting

Based on the results of Wenger *et al.* (2011), we identified 25 candidate models of bull trout occurrence (Supporting Information SI1). Our model selection and ranking procedure consisted of two steps: (a) eliminating models with no support, and (b) weighting the remaining models. Both steps involved evaluating models based on transferability. The transferability of a species distribution model is gauged by the accuracy of its predictions in a different region or climate (Araújo *et al.*, 2005, Hartley *et al.*, 2006, Peterson *et al.*, 2003, Randin *et al.*, 2006). We used spatial transferability as a surrogate for temporal transferability, reasoning that a model that does not reliably transfer to a different region is unlikely to transfer well to a future climate. Transferability was assessed using a form of non-random cross-validation, in which different portions of the data defined by geographic regions are iteratively withheld from model fitting and used to assess model predictive ability (Wenger & Olden, 2012). We conducted a three-fold assessment, meaning that the data were divided into three geographic groups and one group was withheld at a time. Our metric of predictive ability was the area under the curve (AUC) of the receiver-operator characteristic plot, an unbiased and commonly-used performance summary for species distribution models (Guisan & Zimmermann, 2000, Manel *et al.*, 2001). To calculate the probability that each model was the best—i.e., had the highest model weights—we created numerous bootstrap resamples of the dataset, assessed the transferability of each model with each resample, and counted the number of times each model had the highest transferability (i.e., highest AUC). This method of calculating model weights has been proposed several times by statisticians (Buckland *et al.*, 1997, Sauerbrei & Schumacher, 1992, Veall, 1992) and is described in more detail in Supporting Information SI2. In the first step of model selection we used 1000 bootstrap resamples and identified for removal 14 models with a weight of zero. In the second step we repeated the process with the remaining 11 models, but used 5000 bootstrap resamples to more accurately estimate model weights.

Prediction uncertainty

Our approach to characterizing prediction uncertainty was to make a large number of replicate Monte Carlo predictions from the supported models. For each replicate we followed three steps, which we summarize here and describe in detail in succeeding paragraphs. First, we randomly selected a model to use for prediction. Second, we selected a set of values for the model parameters by random draws from the multivariate normal distribution of fixed effects of the chosen model. Third, we used the selected model and parameter values to make predictions at each stream segment in the NHDplus dataset under recent historical (hereafter, "recent") and future climate conditions. For predictions under recent conditions, we used estimated values for temperature and flow drawn from the same datasets as were used for model fitting. For forecasts, we randomly selected from among three datasets representing alternative future climate scenarios (including temperature and flow variables) available for the region. After repeating these steps for 50,000 replicates, we summarized the total available habitat and the uncertainty around this estimate, as explained below.

Step 1. Model selection (incorporating model uncertainty). For each replicate prediction, we randomly selected one of the 11 bull trout models. The probability that each model was selected was given by its weight; thus, a model with a weight of 0.05 had a 5% chance of being selected in any given replicate, and was used in approximately 5% of all replicates. This approach to multimodel inference is essentially the same as that used in Bayesian model averaging (Hoeting *et al.*, 1999), wherein predictions from multiple models are weighted by the posterior model probabilities (i.e., the weights) and combined. It differs from the kind of model averaging described by Burnham and Anderson (2002), in which a single hybrid model is created by weighted averaging of the parameters of individual models. The approach we used is consistent with the ensemble modeling approach advocated by Araújo and New (2006).

Step 2. Parameter selection (incorporating parameter uncertainty). Once a model was chosen, we randomly selected a value for each fixed effect from the multivariate normal distribution of all fixed effects. A multivariate normal distribution must be used because model parameters are rarely independent; some or all co-vary to a degree, so it is not appropriate to make random draws for each parameter independently. The parameters of the multivariate normal distribution are given directly in the model outputs for nearly all statistical analysis software: the means are the mean parameter estimates, and the variances and covariances are given in the parameter variance-covariance matrix.

Step 3. Prediction (incorporating climate uncertainty and residual error). We used the selected model and parameter estimates to make predictions of occurrence probability (which we interpreted as habitat suitability) for all 56,981 stream segments in the study area. We made three sets of predictions: the first under recent conditions, the second under projected climate conditions in the 2040s, and the third under projected climate conditions in the 2080s. Recent conditions referred to the time frame of data collection (1985-2004) which roughly coincided with the baseline period for the climate and hydrologic modeling (the 1980s; Elsner *et al.*, 2010). For predictions for this time period we used the same dataset for temperature and flow as was used for model fitting, along with other relevant covariate values (slope, distance to the nearest unconfined valley bottom, and brook trout presence) for each stream segment. The values of these observed covariates were assumed to be known without error (see Discussion for more on this assumption).

For forecasts under future climate conditions, we had three different sets of projected values for air temperature and flows for the 2040s, and three values for the 2080s; thus, there was uncertainty in future conditions. Each of the datasets was based on the A1B greenhouse gas emissions trajectory (IPCC, 2007), but was generated by a different general circulation model, or combination of models. The first was the mean of the 10 IPCC models with the lowest bias in simulating observed climate conditions across the region (Littell *et al.*, 2010); we refer to this as the composite model, which was used to generate the composite dataset. The second was a single model (PCM1) that predicted relatively little warming and high summer precipitation, and the third was a single model (MIROC 3.2) that predicted relatively high warming and low summer precipitation. The second and the third models bracketed the range of potential future climate conditions that could be associated with other warming trajectories (e.g., B1, A2); each model was used to produce one dataset. We assumed that the composite dataset represented a best approximation and that each bracketing model dataset (i.e., the dataset produced by PCM1 and the dataset produced by MIROC3.2) was less likely than the composite. We therefore assigned a 50% probability to the composite dataset and a 25% probability to each of the bracketing datasets. For each replicate prediction for the 2040s and 2080s we selected one future climate dataset based on these probabilities, and made predictions at each stream segment using the corresponding values for air temperature and flow metrics.

We incorporated random effects into the predictions in two ways. For predictions at sampled locations under recent conditions, we included the subwatershed-specific random effect values (thus, these predictions were considered conditional; Welham *et al.*, 2004). We used a different approach for predictions in unsampled subwatersheds under recent conditions as well as all subwatersheds under future conditions. For these predictions the random effect values were unknown, but assumed to be drawn from a normal distribution (not a logistic distribution as might be supposed; Gelman & Hill, 2007) with a mean of zero and a variance parameter estimated by the fitted model. For every set of predictions we drew one random value from this distribution for each subwatershed, and added this value to the logit-scale predictions for all stream segments in that subwatershed. These predictions were *marginal* as they were not conditioned on estimated random effect values (Welham *et al.*, 2004). For marginal predictions the random effect is part of the residual error, along with the latent residual error at the data level (which in logistic regression is fixed at a variance of $\pi^2/3$). At the end of step 3 we converted all predictions to probabilities on the 0-1 scale using the inverse logit transform, which is equivalent to calculating the probability density of the logistic distribution (with scale parameter of 1) that is greater than zero.

Summing total suitable habitat. We repeated each of the three steps 50,000 times, producing 50,000 replicate predictions of bull trout occurrence probability at each stream segment for recent, 2040s and 2080s timeframes. We considered these predicted occurrence probabilities to represent habitat suitability for the species, and we wished to sum the total suitable habitat across the study area for each of the three scenarios. To do this, we made a random Bernoulli draw of one or zero (representing presence or absence) for each of the 50,000 replicates for each stream segment, based on the predicted occurrence probability for that replicate. This created a matrix of zeros and ones, with each row representing an individual segment, and each of the 50,000 columns representing a replicate prediction. We multiplied each row of the matrix by the length of the stream segment it represented, and then summed the columns. This produced 50,000 replicate predictions of total occupied stream length. From these we calculated the 2.5%, 5%, 50%, 95% and 97.5% quantiles. We also extracted the individual segment-level predictions of occurrence probability that corresponded to each of these quantiles so they could be mapped. Finally, we calculated mean "certainty" at the stream segment scale: how close a prediction was to either one (highly certain presence) or zero (highly certain absence). We calculated this as mean (0.5 + |probability-0.50|). We repeated this process for each of the recent, 2040s and 2080s timeframes.

Sensitivity analysis

We conducted a sensitivity analysis to study the influence of each of the sources of uncertainty on overall uncertainty in total suitable habitat. To do this, we iteratively repeated the analysis for each of the timeframes using only one of the following uncertainty sources at a time: parameter uncertainty, model uncertainty, and climate uncertainty. To exclude parameter uncertainty we used only the mean parameter estimates. To exclude model uncertainty we used only the highest-weighted bull trout model. To exclude climate uncertainty we used only the composite climate dataset.

We included residual error—both at the stream segment scale and at the subwatershed scale, where appropriate—in all the above predictions. We did this because omitting residual error would make predictions 100% certain, resulting in odd model behavior and biased results. We therefore conducted a separate analysis of the role of residual error on prediction uncertainty, focusing particularly on the consequences of omitting the estimated random effect variance from predictions.

We conducted all analyses with the statistical software R (R Development Core Team, 2012). We provide code for the analyses in Supporting Information SI3. The dataset is included as Supporting Information SI4.

Results

Of the 11 models used to predict bull trout occurrence probability, the best-supported model had 51.5% weight and included mean summer temperature, winter high flow frequency, distance to the nearest unconfined valley bottom, and baseflow (Table 1). The next-best model was the same, but lacked baseflow. Temperature and winter high flow frequency appeared in all the models; valley bottom distance appeared in all but two; slope was in five models; brook trout occurrence was included in only two models. Variance of the subwatershed-scale random effect ranged from 3.4 to 4.1, slightly exceeding variance at the data level. Model transferability assessments showed AUC values ranging from 0.733 to 0.763. Values in this range indicate good (but not excellent) predictive performance (Swets, 1988).

For recent conditions, mean estimates of occurrence probability ranged from near zero to near one, with the highest-probability stream segments located at high elevations (Fig. 2a). Uncertainty in mean occurrence probability was often substantial, as illustrated by the histograms for two example streams segments with contrasting habitat conditions (Fig. 3a and

3d). Occurrence probabilities shifted lower in the 2040s and 2080s scenarios (Fig. 3b, 3c, 3e and 3f). For some specific stream segments we observed multimodal distributions, especially in the 2040s and 2080s (e.g., Fig. 3f). This was driven mainly by differences among climate datasets, and to a lesser extent by differences among the bull trout models. In Fig. 3f the three peaks correspond to predictions using the MIROC 3.2 dataset on the left, the composite dataset (which predicts warming nearly as great as the MIROC3.2 dataset for the region) in the middle, and the PCM1 dataset on the right. The PCM1 dataset was associated with substantially less warming in this region than other datasets, and so corresponds to higher probability of bull trout occurrence in the future.

Maps of occurrence probability showed a substantial decline from recent conditions to the 2040s and 2080s (Fig. 2b and 2c). For the 2040s even moderately suitable habitat was limited to higher elevations, and for the 2080s potentially suitable streams were limited to those draining the highest terrain. We found that the total amount of suitable habitat declined from a mean of 36,127 stream km under recent conditions, to 11,251 km under 2040s conditions, and to 2,898 km under 2080s conditions (Table 2). Under nearly best-case conditions (the 97.5% quantile, mapped in Fig. 2d and 2e), bull trout were predicted to persist in central Idaho and isolated high-elevation areas of Montana. The uncertainties around the mean predictions were large (Fig. 4, Table 2), particularly in the 2040s. The histograms of total suitable habitat displayed multimodality, which resulted mainly from differences among species models under recent conditions, differences among climate datasets under 2080s conditions, and differences among both species models and climate datasets under 2040s conditions. The mean certainty of predictions at the stream segment scale was lowest under recent conditions (Table 2) and increased substantially under future climate projections. This was driven by the increasing numbers of stream segments where bull trout were predicted to be absent with a high degree of certainty.

Our predictions showed that the degree of certainty varied spatially and temporally. Under current conditions, bull trout were predicted to be present with high certainty at high elevations (e.g., Fig. 3d, which is a high elevation stream), and absent with high certainty at low elevations. At intermediate elevations (e.g., Fig. 3a), uncertainty tended to be high. Projections for most high elevation locations became less certain in the 2040s and 2080s (Fig. 3e and 3f), while certainty increased at mid-elevation sites as absence became more likely (Fig. 3b and 3c).

The sensitivity analysis showed that differences among the climate datasets (i.e., among the climate models) represented the largest source of uncertainty in total suitable habitat in the 2040s and 2080s (Fig. 5). Both parameter uncertainty and model uncertainty contributed strongly to total uncertainty under recent conditions, but became relatively less important under future climate conditions. In a separate analysis we found that residual error had a minor influence on total suitable habitat uncertainty, which was expected because these errors were modeled as independent at the stream segment scale (for data-level residual error) or subwatershed scale (for the random effect). Technically these errors were binomially distributed; in common language, it suffices to say that the many random errors tended to cancel one another out. However, this residual error was a dominant determinant of mean *segment-scale* uncertainty (as opposed to uncertainty in total suitable habitat). We also found that when residual error was reduced by omitting the random effect, estimates of total suitable habitat were biased low. This was because reducing residual error pushed occurrence probabilities closer to zero and one; since there were more locations with low probabilities than high probabilities in all timeframes, the result was a net reduction in the estimate of suitable habitat.

Discussion

We have demonstrated an approach to modeling uncertainty in species distributions that accounts for uncertainty within models, among models, and in future climate conditions. To our knowledge this is the first example of a comprehensive probabilistic ensemble modeling approach to estimating species distributions under future climates. The resulting forecasts, which take the form of frequency histograms that can be easily summarized, can be valuable tools for studying and communicating the diversity of potential outcomes for a species at a specific location or range-wide. The methods are readily adapted to other applications, such as projections of species invasion potential or responses to land use change.

In our example with bull trout we found that despite large uncertainty in future climate conditions, the scenario outcomes became increasingly certain at the stream segment scale. This was because an increasing proportion of locations became definitively unsuitable for bull trout, regardless of the climate dataset or species model considered. Apparently the species is already living at the edge of its niche space in this geographic region, and any increase in unfavorable conditions (rising temperatures and increasing winter high flows) led to a net decline. Under 2080s conditions, it was likely that the species would be confined to less than 5,000 km of suitable habitat, and almost certainly less than 10,000 km of suitable habitat. The pattern of increasing certainty that we observed is likely to be typical of high-elevation species with limited potential to migrate, such as those on mountaintop habitat "islands"(McDonald & Brown, 1992).

Past examinations of uncertainty in SDMs (Barry & Elith, 2006, Beale & Lennon, 2012) focused on the underlying causes of high uncertainty, such as false absences, missing covariates, small sample size, and errors in measures of covariates. We agree that it is important to understand these causes and try to minimize errors. However, some degree of error and uncertainty is inevitable, and these errors are built into many modeling frameworks. Our goal was to develop methods that thoroughly accounted for the uncertainties associated with predictions from one class of models (GLMs/GLMMs), so that the resulting uncertainties could be communicated along with the mean predictions, and so that we could derive valid estimates of prediction intervals for total suitable habitat under future conditions.

It is worth asking whether we have indeed accounted for all major classes of uncertainty. In particular, one might question the assumption that most predictor variables (except those representing future climate conditions) are known without error. Although not literally true, there is normally no need to model these errors because any uncertainty in the measurement or estimation of an independent variable adds noise to the dataset, which tends to increase other types of model error, and these other errors *are* modeled and propagated into prediction uncertainty using our methods. Thus it would be redundant to model measurement error separately. Measurement error also reduces (attenuates) the magnitude of the associated parameter estimate, which can be a problem under certain circumstances (Warton *et al.*, 2006). Most of the time, however, this bias is not of practical concern for prediction as long as the measurement error rate is the same for the predicted variables as the observed variables, which should normally be the case (Barry & Elith, 2006, Warton *et al.*, 2006).

Another source of uncertainty sometimes considered by researchers is data uncertainty (Buisson *et al.*, 2010, Dormann *et al.*, 2008a, Roura-Pascual *et al.*, 2009). This is typically addressed by iteratively parameterizing models using different random subsets of the data. While we see value in the use of data subsets for model evaluation and model weighting, we argue that discarding a portion of the data for each forecast is overly conservative under most circumstances. Once a set of models has been selected and weighted, the full dataset is the most appropriate source of information for model fitting and calculation of parameter error and residual error (Fielding & Bell, 1997, Hartley *et al.*, 2006). An exception might be made if some data points are of questionable reliability and there is an interest in exploring their influence on results (e.g., Dormann *et al.*, 2008a).

There is one source of uncertainty that is important, yet cannot be modeled: uncertainty due to misspecification of *all* models. If there are important predictor variables that have not been considered or measured, or if the form of the predictor-response relationship is grossly misspecified (e.g., modeling a quadratic relationship as linear), then predictions could be biased to an unknown degree. For example, quantitative information on fish response to fire and post-fire disturbance is limited (Luce *et al.*, 2012), and there is substantial uncertainty about whether fire frequency and severity will increase with climate warming (Holden *et al.*, 2011), so fire frequency was not included as a candidate predictor in our models. We suspect any bias associated with this omission is small, but this remains untestable at this time.

Although we used frequentist methods, the statistical foundation for the kind of multimodel averaging we employed lies in Bayesian model averaging (Hoeting *et al.*, 1999, Kass & Raftery, 1995). Bayesian model averaging says that for a set of models M and data D, the prediction $pr(\Delta|D)$ is the sum of individual predictions from each model $pr(\Delta|M_k,D)$ multiplied by its associated model weight $pr(M_k|D)$:

$$pr(\Delta|D) = \sum_k pr(\Delta|M_k,D)\,pr(M_k|D)$$

Thus, the full prediction is a weighted average of individual model predictions. An alternative model averaging approach is to create a single hybrid model of all the individual models by averaging their parameters (Burnham & Anderson, 2002), and to predict from this single model. These two approaches can be thought of as "prediction averaging" and "parameter averaging." We find the prediction averaging approach more intuitive for this purpose, as it allows multiple competing hypotheses to be expressed as separate models, whose predictions are combined to express the range of possible outcomes, rather than creating a single hybrid model that embodies many (possibly mutually exclusive) hypotheses at once.

We evaluated our candidate models on the basis of transferability, the ability of models developed in one geographic region to predict species occurrence in another geographic region successfully. This approach is increasingly common with species distribution models (Dobrowski *et al.*, 2011, Heikkinen *et al.*, 2012, Tuanmu *et al.*, 2011), and we argue that it provides potential insight into model performance under future climates; if a model cannot predict well in a new geographic location, we cannot have faith that it will predict well under new climate conditions in the same geographic location. A key reason for spatial and temporal variability in performance is that environmental (predictor) variables occur in different combinations, and their correlations likewise vary. One challenge in ranking models by transferability is how to calculate the model weights. Commonly-used approaches for calculating model weights rely on the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) or similar metrics calculated from the model likelihood using the fitting dataset. These criteria cannot be calculated using a performance-based measure such as transferability. Hartley et al. (2006) resolved this by using an *ad hoc* scoring system based on transferability performance. We used an approach based on bootstrapping. Although this was not particularly difficult (as described in Supplement 2), others may wish to use the more conventional approaches based on AIC and BIC to generate model weights.

Our approach can be generalized to models other than GLMs and GLMMs. Climate uncertainty is straightforward to address regardless of modeling method, and model uncertainty can be addressed in part by considering different subsets of predictor variables, or using multiple modeling methods. There are numerous examples where these sources of uncertainty have been examined (e.g., Buisson *et al.*, 2010, Diniz-Filho *et al.*, 2009, Pearson *et al.*, 2006). Fully accounting for within-model uncertainty (i.e., the analog to parameter uncertainty in GLMs) is less common and more challenging with machine learning and other flexible methods. Some methods may be more amenable to this than others: for example, random forests (Breiman, 2001) internally produces numerous classification trees, which together should describe the within-model uncertainty. The difficulty is in translating this to uncertainty in projections while accounting for other sources of variability. We have not yet explored this.

One important question is how to best communicate the uncertainty in species distributions captured by these methods. Although it is impractical to show the full distributions of occurrence probability (Fig. 3) for all locations, the mean estimate (mapped in Fig. 2A-C) captures the most critical information, as probability values farther from zero and one are inherently less certain. It can also be interesting to examine the full uncertainty distributions for selected locations. For example, the bimodality shown in Fig. 3F is not necessarily an intuitive result, and suggests two distinct possible trajectories for bull trout in this stream. For summary measures, such as total suitable habitat, we recommend histograms such as those shown in Fig. 4. These can also be constructed for any geographic subset of interest. At a minimum, however, we argue against converting maps of occurrence probability to maps of presence-absence. Although this is still quite common, it completely discards all uncertainty information, and it gives a false sense of confidence in predictions.

Three limitations of our example must be mentioned. The first is that we used just three future climate datasets, because these were the only ones available with accompanying hydrologic projections across the study area. Other studies have employed a larger number of climate datasets by using multiple models and multiple emissions trajectories (Bagchi *et al.*, 2013, Buisson *et al.*, 2010) or even resampled from an ensemble climate forecast of 21 models (Fronzek *et al.*, 2010). More datasets are desirable, and it is unlikely that our projections represented all reasonable combinations of temperature and flow change. However, the bracketing models did encompass a broad range of predicted increases in air temperature (mean 2.49-5.51 °C increase by the 2080s), and, though larger increases are possible, increases smaller than this range are unlikely given current emissions trajectories (Peters *et al.*, 2013) . The second limitation is the use of air temperature in lieu of stream temperature. Air temperature is an imperfect surrogate (Mayer, 2012) and in particular does not account for localized cold-water refugia produced by groundwater inputs (Arismendi *et al.*, 2012). However, while the use of air temperature undoubtedly contributes to model uncertainty, it should not otherwise cause model bias unless such coldwater refugia become relatively more common in the future. The third limitation is that we ignored the spatial arrangement of habitat fragments. In reality, many potentially suitable habitat segments will be located in isolated locations and will be too small to sustain populations over time (Roberts *et al.*, 2013). This limitation implies that our forecasts of suitable habitat could be optimistic.

There is increasing recognition that uncertainty in species distributions should be taken into consideration in conservation planning and reserve design (Bagchi *et al.*, 2013, Carvalho *et al.*, 2011, Moilanen *et al.*, 2006). A probabilistic approach to uncertainty is particularly valuable in estimating the strength of evidence for species extinction at local and regional scales—information that is of critical conservation importance. For bull trout, there are many areas where the amount of suitable habitat is projected to be near zero, with >95% certainty, even by the 2040s. These are likely to be poor conservation investments. In contrast, areas where the amount of suitable habitat is highly uncertain in coming decades may be important locations to monitor, and potential candidates for restoration activities that could offset climate warming effects. In cases such as this, in which a climate-sensitive species faces range-wide decline, a probabilistic understanding of uncertainty is essential for directing limited resources to the locations where they have the greatest potential for conservation benefit.

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Geological Survey Forest and Rangeland Ecosystem Science Center, and the U.S. Fish and Wildlife Service. The fish data used in this study were compiled from multiple sources, including a previous database of sites in the range of westslope cutthroat trout (Rieman *et al.*, 1999), which included data from the Idaho Department of Fish and Game's General Parr Monitoring database and other sources. Additional data were provided by Bart Gammett of the Salmon-Challis National Forest, Joseph Benjamin of the US Geological Survey, Kevin Meyer of the Idaho Department of Fish and Game, and Brad Shepard of the Wildlife Conservation Society. Use of trade or firm names in this manuscript is for reader information only and does not constitute endorsement of any product or service by the U.S. Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of federal agencies.

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Supporting Information Legends

SI1. CandidateModels.docx. List of 25 candidate models to explain bull trout occurrence.

SI2. BootstrapMethods.docx. A summary of bootstrap methods used to calculate model weights.

SI3. Rcode.txt. R code for implementing the methods described in this article.

SI4. Dataset.zip. The bull trout dataset used as an example in this article. Eight files are included: the bull trout data used to fit models (newbull.csv), data to make predictions across the study area under recent (historical) conditions (bdhist.csv), data to make predictions for the 2040s timeframe (bd2040c.csv, bd2040m.csv, bd2040p.csv) and data to make predictions for the 2080s timeframe (bd2080c.csv, bd2080m.csv, bd2080p.csv).

Table 1. The top 11 bull trout models, with model weights and mean AUC score based on transferability.

Model	Weight	Transferability AUC
temp + winterflow + valleybottom + baseflow	51.5%	0.763
temp + winterflow + valleybottom	27.1%	0.758
temp + winterflow + valleybottom + baseflow + baseflow^2	6.7%	0.757
temp + winterflow + slope + valleybottom + baseflow	4.6%	0.755
temp + winterflow + slope + valleybottom + baseflow + baseflow^2	3.4%	0.752
temp + winterflow + slope + valleybottom	2.3%	0.751
temp + winterflow + valleybottom + brooktrout	1.2%	0.739
temp + winterflow	1.0%	0.737
temp + winterflow + baseflow	1.0%	0.738
temp + winterflow + slope + valleybottom + baseflow	0.6%	0.733
temp + winterflow + slope + valleybottom + baseflow + brooktrout	0.6%	0.733

Table 2. Mean certainty of predictions at the segment scale and estimated total length of suitable habitat under recent conditions, 2040s climate projections and 2080s climate projections.

Timeframe	Segment-scale certainty	Kilometers of suitable habitat		
		2.5% quantile	Mean	97.5% quantile
Recent	77.9%	30,144	36,127	42,500
2040s	88.5%	5,268	11,251	18,914
2080s	98.8%	496	2,898	7,946

Figure Legends

Figure 1. Study area. Sample sites are indicated as circles. The two stars are the locations of streams used as examples in Figure 3.

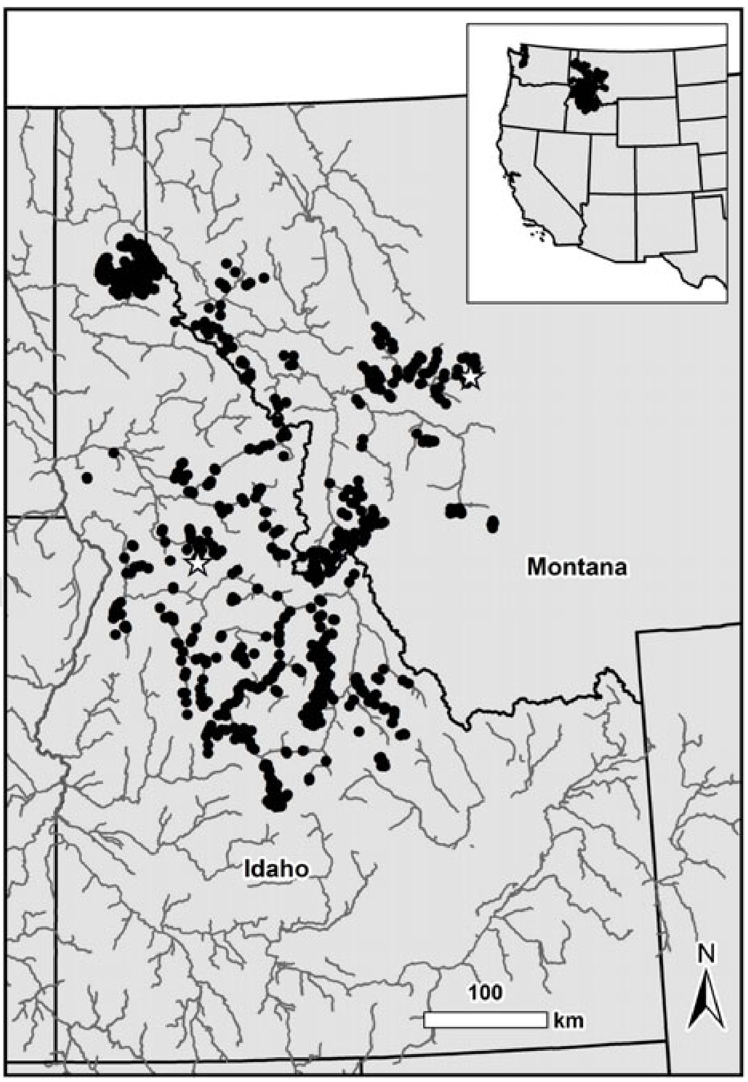
Figure 2. Mean projected occurrence probability (habitat suitability) for bull trout under recent conditions (a), 2040s climate projections (b) and 2080s climate projections (c). Also shown are the 97.5% quantiles for the 2040s (d) and 2080s (e), representing nearly best-case conditions for projections. Dark grey shading indicates regions outside of the study area.

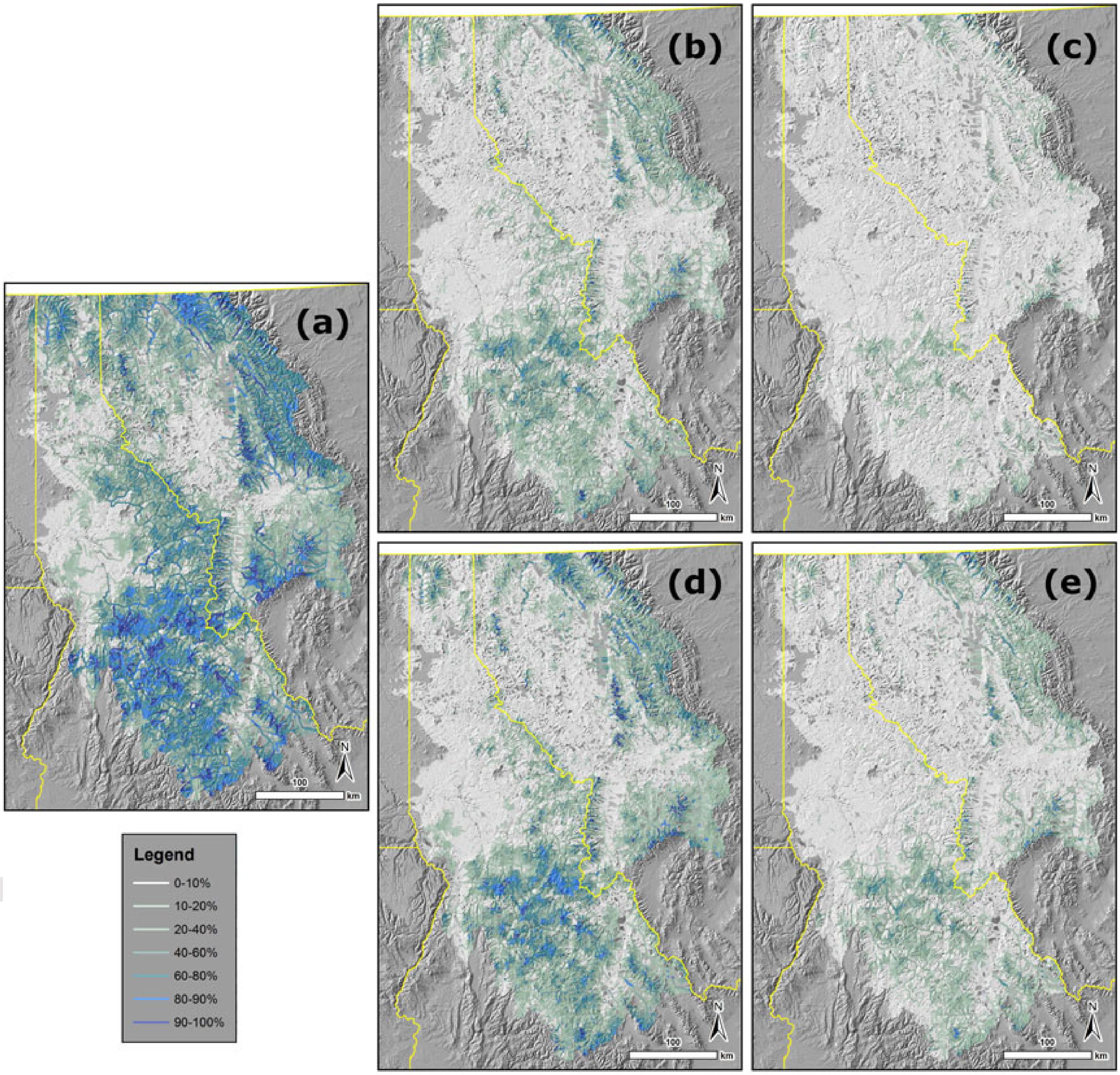
Figure 3. Example histograms of predicted occurrence probability (habitat suitability) for two individual stream segments under three scenarios, based on 50,000 Monte Carlo predictions for each. The first stream segment, shown in panels a through c, is on the Crooked River, a mid-elevation tributary to the Clearwater River (indicated on Fig. 1 as the star within the state of Idaho). The second segment, shown in panels d through f, is a high-elevation segment of the Blackfoot River headwaters (indicated on Fig. 1 as the star within the state of Montana). Colors

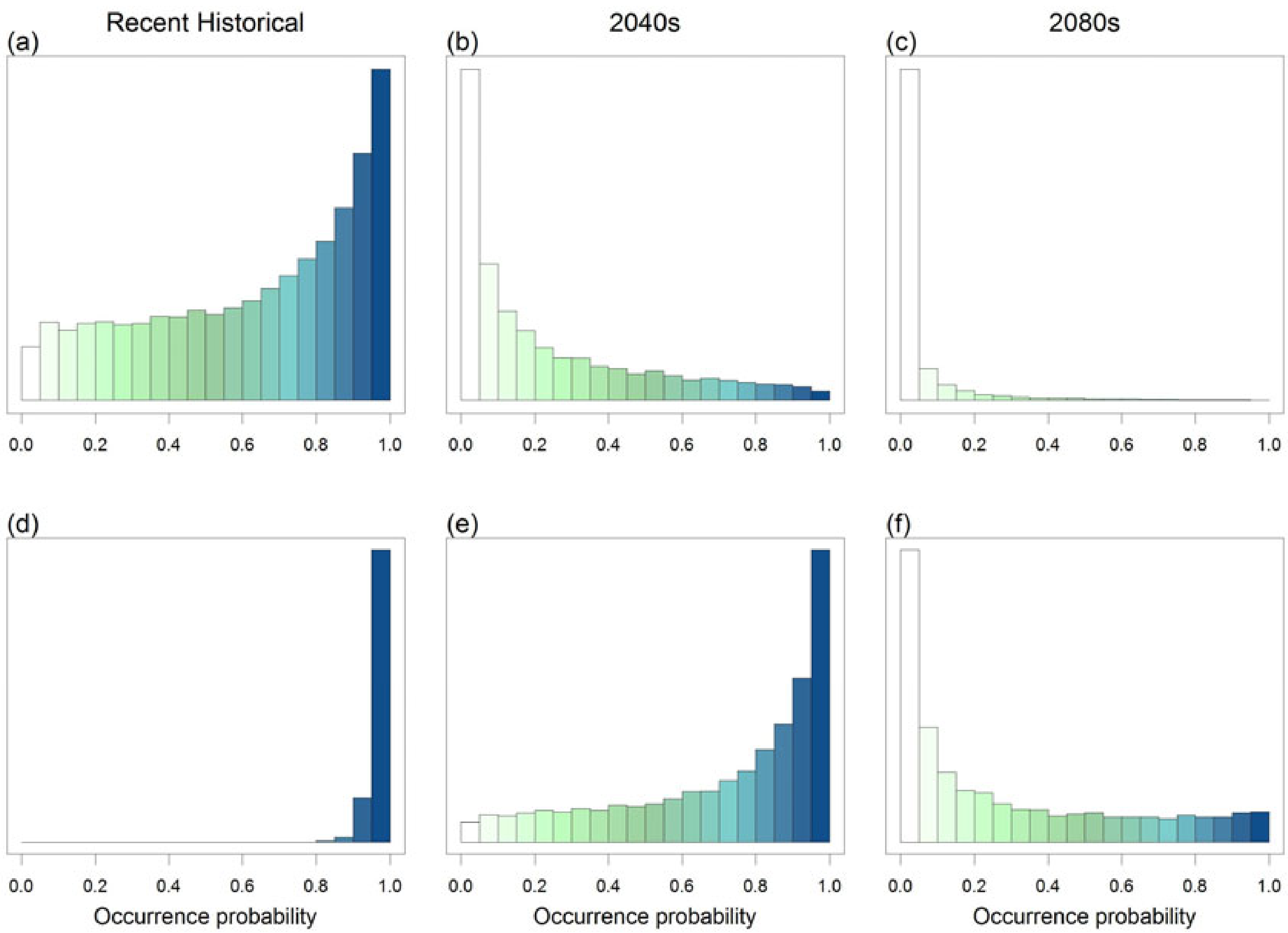
correspond to those in Fig. 2. These histograms reflect uncertainty due to parameter uncertainty, model uncertainty, and climate uncertainty, but do not include uncertainty due to the random effect.

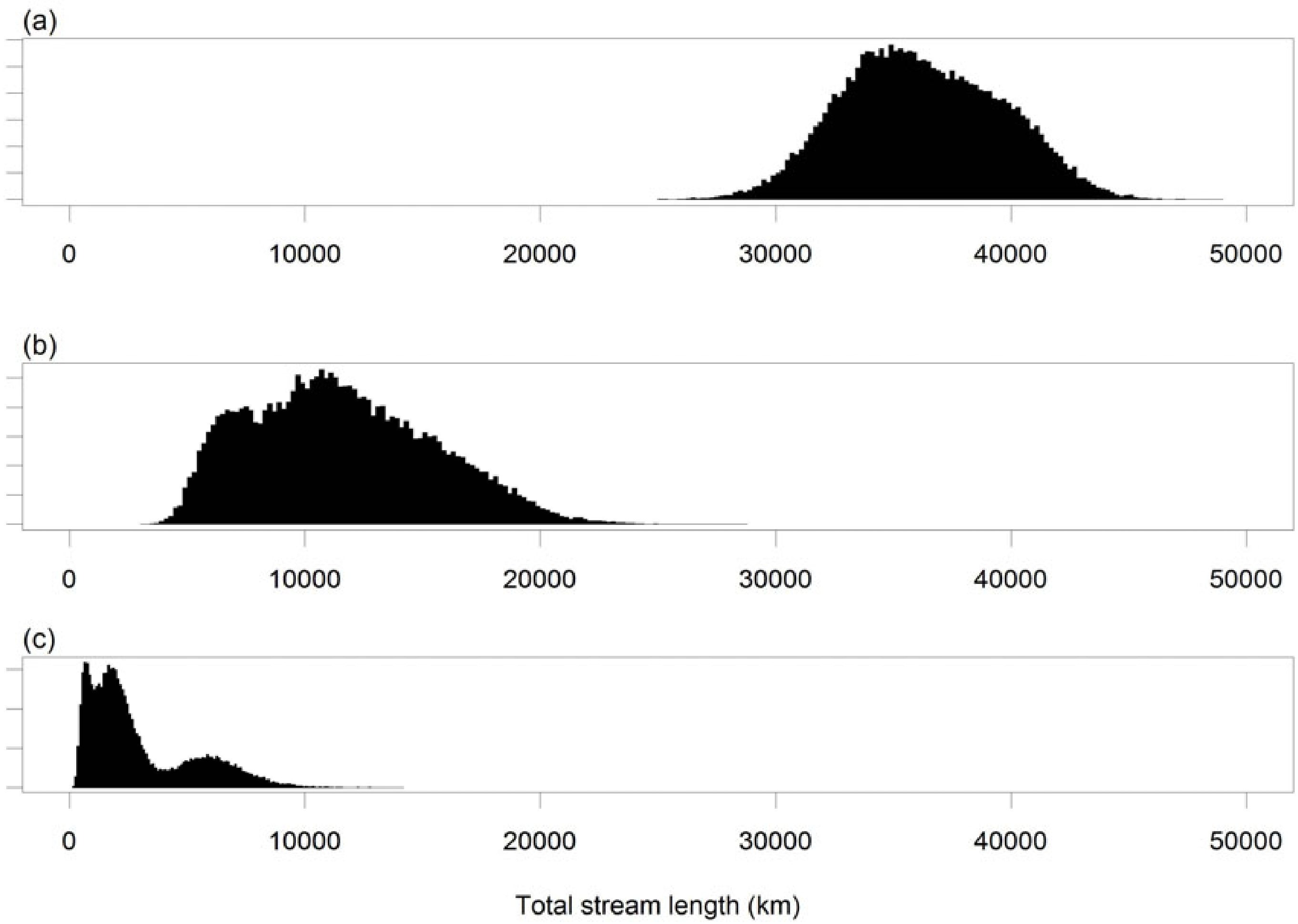
Figure 4. Histograms of 50,000 replicate estimates of total suitable habitat for bull trout under recent conditions (a), 2040s climate projections (b) and 2080s climate projections (c).

Figure 5. Results of sensitivity analysis, showing the 95% intervals of suitable habitat for the full models and each of the reduced models for the recent, 2040s and 2080s timeframes. The wider the band, the greater the uncertainty contributed by that source.




(a)
(b)
(c)
(d)
(e)
N
100
km
Legend
0-10%
10-20%
20-40%
40-60%
60-80%
80-90%
90-100%


Recent Historical
2040s
2080s
(a)
(b)
(c)
(d)
(e)
(f)
0.0
0.2
0.4
0.6
0.8
1.0
Occurrence probability


(a)
0
10000
20000
30000
40000
50000
(b)
0
10000
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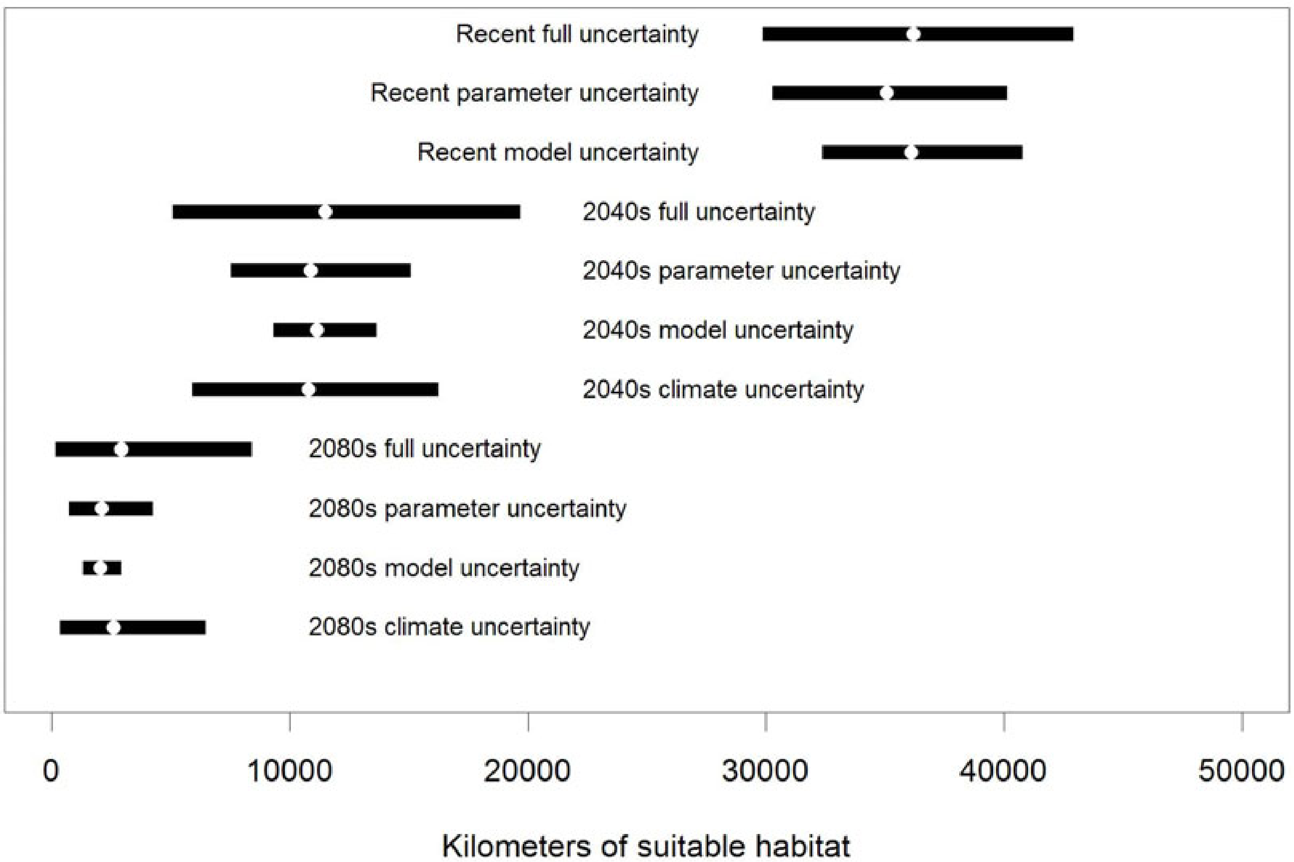
40000
50000
(c)
0
10000
20000
30000
40000
50000
Total stream length (km)


Recent full uncertainty
Recent parameter uncertainty
Recent model uncertainty
2040s full uncertainty
2040s parameter uncertainty
2040s model uncertainty
2040s climate uncertainty
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2080s model uncertainty
2080s climate uncertainty
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10000
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Kilometers of suitable habitat