

ARTICLE

# Geographic Variability in Elevation and Topographic Constraints on the Distribution of Native and Nonnative Trout in the Great Basin

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## Abstract

Understanding local and geographic factors influencing species distributions is a prerequisite for conservation planning. Our objective in this study was to model local and geographic variability in elevations occupied by native and nonnative trout in the northwestern Great Basin, USA. To this end, we analyzed a large existing data set of trout presence (5,156 observations) to evaluate two fundamental factors influencing occupied elevations: climate-related gradients in geography and local constraints imposed by topography. We applied quantile regression to model upstream and downstream distribution elevation limits for each trout species commonly found in the region (two native and two nonnative species). With these models in hand, we simulated an upstream shift in elevation limits of trout distributions to evaluate potential consequences of habitat loss. Downstream elevation limits were inversely associated with latitude, reflecting regional gradients in temperature. Upstream limits were positively related to maximum stream elevation as expected. Downstream elevation limits were constrained topographically by valley bottom elevations in northern streams but not in southern streams, where limits began well above valley bottoms. Elevation limits were similar among species. Upstream shifts in elevation limits for trout would lead to more habitat loss in the north than in the south, a result attributable to differences in topography. Because downstream distributions of trout in the north extend into valley bottoms with reduced topographic relief, trout in more northerly latitudes are more likely to experience habitat loss associated with an upstream shift in lower elevation limits. By applying quantile regression to relatively simple information (species presence, elevation, geography, topography), we were able to identify elevation limits for trout in the Great Basin and explore the effects of potential shifts in these limits that could occur in response to changing climate conditions that alter streams directly (e.g., through changes in temperature and precipitation) or indirectly (e.g., through changing water use).

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The range of a species can be most fundamentally described in terms of geography (latitude and longitude) and elevation (Peters 1988; Parmesan 2006; Chen et al. 2011). These factors reflect the underlying influences of climatic conditions on potential species distributions, defining what is often described as a bioclimatic envelope (Heikkinen et al. 2006). Within such

limits, the actual or realized distribution of a species may be constrained by a variety of local factors (Soberón and Nakamura 2009). Understanding these factors represents a major challenge, and often involves analyses at multiple scales (Fausch et al. 1994; Peterson and Dunham 2010). Here, we evaluate climate-related gradients in geography and local constraints

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imposed by topography on the potential and realized elevations occupied by the three of the most common trout species in the northwestern Great Basin (Behnke 1992; Grayson 2011). Specifically, we considered Brook Trout *Salvelinus fontinalis*, Rainbow Trout *Oncorhynchus mykiss*, and Lahontan Cutthroat Trout *O. clarkii henshawi*. Brook Trout is nonnative and of particular concern in regard to its impact on native trout (Dunham et al. 2002). Rainbow Trout is native in only the northern part of our study area but has been commonly introduced in southern streams (Crawford and Muir 2008). Lahontan Cutthroat Trout is a threatened subspecies that is native and present only in the central and southern portion of our study area (Dunham et al. 1999).

The expansive geographic and topographic relief of the Great Basin provides an excellent physical template for generating climate variability (Melack et al. 1997), which in turn strongly controls a variety of species distributions within and among mountain ranges in the basin (Whittaker and Niering 1965; Brown 1971; Fleishman and Mac Nally 2003; Martínez-Meyer et al. 2004; Schoville and Roderick 2009). In these montane ecosystems elevation is a strong local driver of air temperatures and precipitation, and at a broader extent, climatic conditions across the Great Basin track gradients of latitude and longitude (Daly et al. 2008; Rowe et al. 2010; Grayson 2011). Although specific local temperatures are difficult to model across the mountainous regions of the Great Basin, strong climate-by-elevation and climate-by-latitude relationships persist across the montane west (e.g., Keleher and Rahel 1996; Melack et al. 1997; Dunham et al. 1999). Keleher and Rahel (1996), for example, found that 77% of the variability in mean July air temperature in Wyoming could be explained by a model that included latitude and elevation. For the Rocky Mountains, 90% of mean July air temperature was accounted for by a quadratic equation that included just latitude and elevation. Dunham et al. (1999) found strong agreement between the downstream limits of Cutthroat Trout and the 18°C thermocline from the Keleher and Rahel (1996) model. With its strong local and regional climatic gradients the Great Basin is well suited to both aquatic and terrestrial studies that evaluate climate impacts on biota and how changes in climate influence populations and communities (see Smith 1978; Grayson 1993; Rowe et al. 2011).

As with many terrestrial species, the elevations occupied by trout in the Great Basin are consistent with expected climate gradients linked to geography (latitude and longitude). Existing work on the influence of climate on trout distributions in the Great Basin region has been either based on limited data sets with a focus on a single species (e.g., Dunham et al. 1999) or based on very broad scales that lack resolution to explore patterns within a specific region (e.g., Keleher and Rahel 1996; Wenger et al. 2011). To address these knowledge gaps, we assembled data from surveys of trout in the northwestern Great Basin to provide a more comprehensive and regionally specific analysis of factors influencing the distributions of the four most common species of trout. Our specific objectives were threefold: (1) define current distribution limits for native and nonnative

trout as a function of latitude, longitude, and local elevation, (2) evaluate evidence for topographic constraints on species distributions within these broader bioclimatic envelopes, and (3) explore the degree of habitat loss that may be expected in response to a range of potential shifts induced by climate change in the downstream elevation limit for trout.

## METHODS

### Study Site

The hydrographic Great Basin encompasses a large region in the western United States that has no current outlet to any ocean (Grayson 2011). In this study, we focused on the northwestern portion of the Great Basin (Figure 1), which is dominated by the Lahontan Basin that held the >15,000-km<sup>2</sup> Lake Lahontan during the last glacial maximum (Benson 1980; Adams and Wesnousky 1999), and also includes the Oregon Lakes region, which contains five separate endorheic basins at the northern extent of the Great Basin region (Figure 1; hereafter referred to as “terminal basins”). The maximum elevation within our study area is 3,590 m and the minimum basin elevation is 1,180 m. The majority of precipitation falls as snow and snow-pack depth has a substantial influence on spring and summer discharges (e.g., Poff and Ward 1989). Weather stations are sparse in this region; but, based on the nearest weather stations mean annual precipitation in the region is about 250 mm (National Oceanic and Atmospheric Administration’s 1981–2010 Climate Normals data set), although precipitation varies widely among localities (Shinker 2010).

The presence of native trout in these desert streams is a legacy of the last glacial maximum when climates were more moderate and large pluvial lakes filled much of the Great Basin (Benson 1980; Behnke 1992; Adams and Wesnousky 1999; Grayson 2011). Four salmonid species (collectively referred to as “trout” hereafter) predominate in the northwestern Great Basin: Lahontan Cutthroat Trout, Rainbow Trout, Brook Trout, and Brown Trout *Salmo trutta*. Lahontan Cutthroat Trout and Rainbow Trout are native to the Lahontan Basin and the Oregon Lakes regions, respectively, whereas Brook and Brown Trout are nonnative throughout. Brown Trout are present but uncommon, occurring in only a few systems. Given their limited abundance and distribution in our study area, we excluded Brown Trout from our analyses. Rainbow Trout are native only to the Oregon Lakes region. Nonnative Rainbow Trout populations have been established in many streams across other portions of the Great Basin, including the Lahontan Basin. The Lahontan subspecies of Cutthroat Trout, which is listed as threatened under the U.S. Endangered Species Act (Coffin and Cowan 1995), does not occur naturally in the Oregon Lakes basins, and our samples only included Lahontan Cutthroat Trout populations from within their native range. Potential hybridization among *Oncorhynchus* species can occur but was not widely observed in our data set. For this study hybridization was categorized as a “presence” for the nonnative species only.

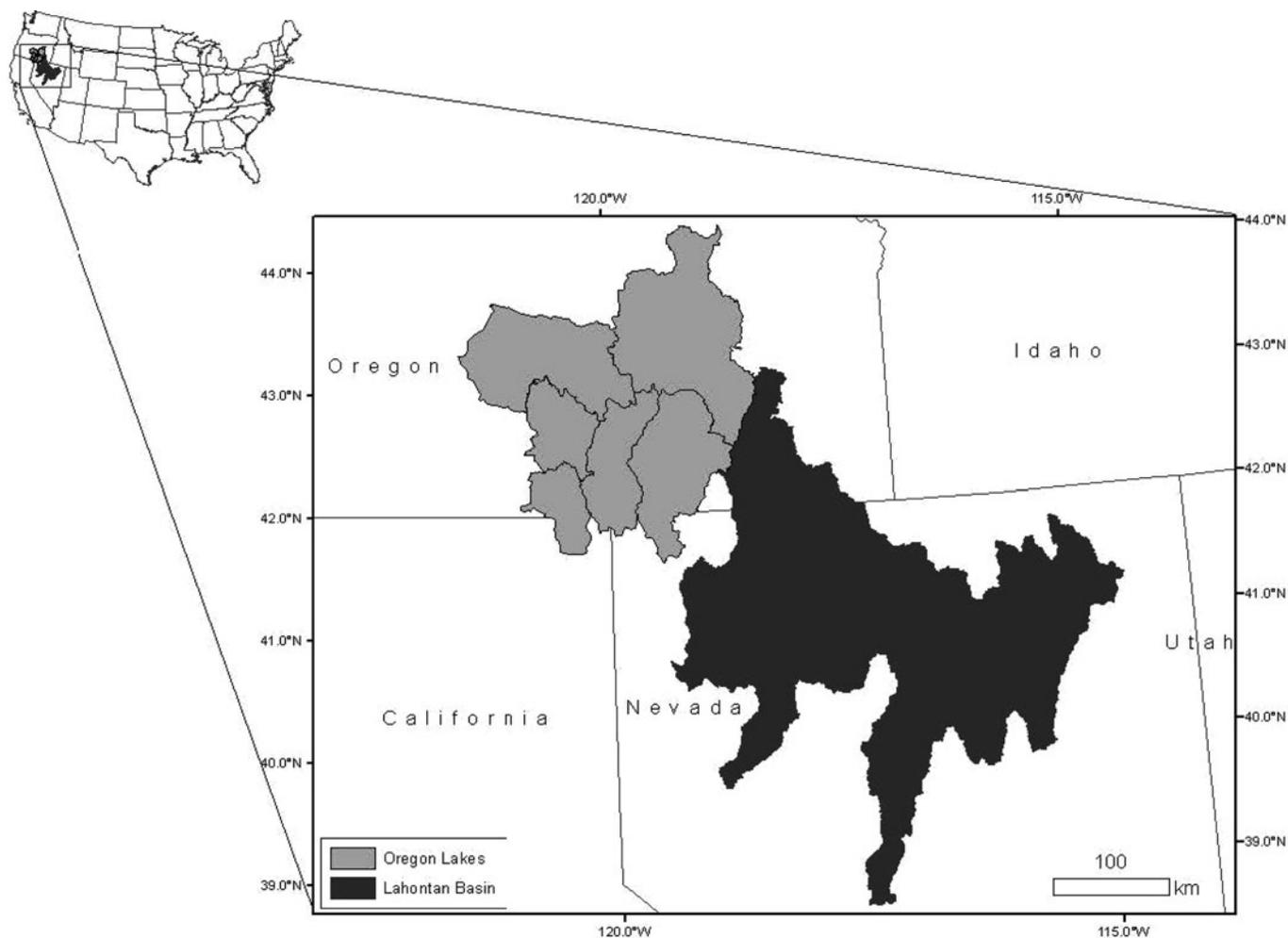


FIGURE 1. The study region in northern Nevada and southeastern Oregon. The eastern Lahontan Basin in which Lahontan Cutthroat Trout are native is shaded dark gray, and the Oregon Lakes basins in which Rainbow Trout are native are shaded light gray. Dark lines indicate independent basins with internal drainage.

### Data Collection

Information on fish presence and absence was derived from 5,156 fish surveys conducted across multiple decades (1953–2010) in more than 500 streams across the study area. All fish surveys were conducted using backpack electrofishing. Stream survey reaches were a minimum of 33 m long. Because elevated flows in spring and early summer could lead to fish occurrence downstream from summer limits, we constrained our analysis to field surveys conducted after July 1 and before October 1 each year. Surveys of fish presence were well distributed geographically within the study area and across all potential elevations, and included areas of fish absence upstream and downstream from the core areas of fish occurrence. Having documented trout absence data as well as trout presence data provided a high degree of confidence that the limits we documented were a product of presence or absence of fish from the stream rather than the presence or absence of a survey at a given site. Although survey details varied over time as study focus

and sampling efforts shifted, all surveys included: (1) a list of trout species captured by backpack electrofishing, and (2) the latitude and longitude of the site. If no trout were observed during the surveys, a zero value was recorded. We assumed a high probability of detection (see Wenger et al. 2011) but could not specifically determine detectability for each location sampled. If a site had fish present at any one time we categorized the site as having that species “present”; however, for sites where multiple surveys were conducted over time with fish present on more than one occasion, we removed all duplicate data points to avoid biasing the quantile analysis with multiple occurrences at the same place (see below). We evaluated data obtained over a long time period (~60 years) because we were most interested in determining a bioclimatic envelope that reflected where trout could potentially occur, and by including all available data we were provided with the broadest picture of fish presence.

We used GIS to determine basic physical characteristics at each site: elevation, basin area, maximum basin elevation,

maximum stream elevation within each basin, elevation of the terminal basin for a given stream, and stream gradient within a larger reach centered on the survey site. Elevation, basin area, and maximum elevation within the basin were determined using digital elevation models (DEMs) in ArcGIS version 10 (Environmental Systems Research Institute, Redlands, California). Maximum stream elevations, in meters, were obtained from the National Hydrography Dataset (NHD) using stream data from the NHDPlus application-ready geospatial data set (NHDPlus User Guide, pages 97–98, [www.horizon-systems.com/nhdplus/documentation.php](http://www.horizon-systems.com/nhdplus/documentation.php)). We used the MaxElevSmo from NHDPlus to obtain the smoothed maximum elevation for each survey reach. “Terminal basin elevation” is the minimum basin elevation, in meters, per eight-digit Hydrologic Unit Code subbasin (HUC\_8; see NHDPlus User Guide, page 31, for definition) and was estimated by applying the Zonal Statistics as Table tool in ArcGIS to the NHDPlus DEMs and the Watershed Boundary Dataset (U.S. Department of Agriculture, National Resources Conservation Services, <http://nhd.usgs.gov/wbd.html>) boundaries for HUC\_8. Gradient was derived by extracting the elevation of points 250 m upstream and downstream from the study site from a 10-m (Oregon) or 30-m (Nevada) DEM and then calculating rise (elevation difference) over run (stream distance between elevation points).

### Data Analysis

*Delineation of bioclimatic envelopes.*—We evaluated the edges of trout distributions across the northwestern Great Basin using quantile regression (Cade et al. 1999; Cade and Noon 2003) applied via the “proc quantreg” command in the SAS software program, version 9, of the SAS System for Windows (SAS Institute, Cary, North Carolina). For Rainbow Trout, we considered distribution limits of the native (Oregon Lakes region) and nonnative (Lahontan Basin) ranges separately. Quantile regression determines a conditional relationship (a linear relationship in this case) for which a given proportion of the data in that distribution occur at or below a specified quantile. For example, regression along the 5th quantile determines the linear relationship between the dependent and independent variables for which 5% of the data fall at or below a given line. Similarly the 95th quantile regression in our analysis would be a linear relationship between a dependent variable and one or more independent variables for which 95% of the data occur at or below that line. Quantile regression analysis is particularly useful for quantifying relationships at the edge of a distribution because it is largely insensitive to outliers and can be applied without assuming specific error distributions (i.e., error can be homogeneous or heterogeneous and need not be normally distributed; Cade et al. 1999; Cade and Noon 2003). Details on quantile regression and its application to ecological data are discussed in greater detail in Cade et al. (1999) and Cade and Noon (2003).

Quantile regression is well suited to quantifying distribution edges in a large data set such as ours, which encompasses a full range of species occurrences across a landscape (Terrell et al.

1996; Flebbe et al. 2006; Vaz et al. 2008). We used a multiple quantile regression analysis with two independent variables, latitude and longitude, to determine the elevation of the upstream (95th quantile) and downstream (5th quantile) distribution limits of each trout species in our study region. Regression along the 95th quantile in our analysis yielded a relationship in which 95% of the sites with fish present occurred at or below a given elevation along a gradient of latitude and longitude. Similarly, regression along the 5th quantile described a relationship between elevation (response variable) and latitude and longitude in which 5% of the sites with fish present occurred below a given line. Using these models, the predicted range of potentially occupied elevation, or bioclimatic envelope, for each species was defined as the range of elevation enveloped within the 5th- and 95th-quantile model predictions. Relationships were considered significant when regression *P*-values were less than 0.05 ( $\alpha = 0.05$ ).

We chose the 5th and 95th quantiles to ensure that slopes and intercepts remained consistent with the larger data set (Figures A.1–A.4 in the Appendix). Although we could have used a slightly larger distribution (more extreme quantile) in some cases, this was not true of all models. By adopting the same quantiles for all models, we could provide consistent comparisons among trout species and scenarios.

*Proportion of overall elevation range occupied.*—We first evaluated the relative importance of latitude and longitude in our analysis of the elevation range occupied by each species. The influence of longitude was often insignificant, and when significant it was small relative to that of latitude (see Results). Based on this initial assessment, we focused our subsequent analysis on gradients driven by latitude, the dominant factor accounting for upstream and downstream distribution limits (95th and 5th quantiles, respectively) for all three species of trout. The difference between the elevation of the downstream distribution limit (5th quantile of the latitude by elevation relationship) and upstream distribution limit (95th quantile) for a given latitude provided an estimate of the total elevation relief that could be occupied at that latitude (hereafter, “elevation range of fish occurrence”). We then compared the elevation range of fish occurrence with the total elevation relief within a given stream system from its headwaters downstream to the terminal basin of the system. We then calculated the proportion of the total elevation relief encompassed by the elevation range of fish occurrence. The estimated proportion of the total relief was then calculated for each species as a function of latitude. For each species, we expected to find a greater proportion of occupied relief in more northerly latitudes due to cooler climatic conditions, which would allow access to lower elevation streams. Among species, we expected native trout to occupy a greater proportion of potentially occupied relief, since nonnative species may not have had enough time to fully colonize potentially accessible habitats.

*Topographic constraints on distributions.*—Quantile regression models allowed us to identify upstream and downstream distribution limits (elevation) along a latitudinal gradient that

are likely to be reflective of influences from the existing climate gradients in the northern Great Basin. In many cases, however, the actual or realized maximum elevation of fish distributions may be limited by maximum elevation of available streams present in a catchment or by impassable stream features such as waterfalls or steep stream gradients: in other words, topographic constraints rather than climatic constraints. Similarly, downstream distributions may be topographically constrained if the terminal catchment elevation is higher than the climatic constraints to the lower elevation limit for a species. To evaluate constraints on the upstream elevation distribution of fish across our study region, we plotted the elevation of all sites with fish present versus maximum elevation of the stream in which it occurs. We then ran a quantile regression for the 95th quantile of the relationship between elevation of all sites with fish present versus maximum elevation to determine whether the relationship between the upper limit of each species distribution was comparable across maximum stream elevations (slope = 1) or if the upstream limit changed with the maximum stream elevation (slopes  $\neq 1$ ). The upper end of intermittent flow identified in the NHDPlus data set represented the maximum upstream potential. While the classification for an intermittent stream using the NHDPlus model carries potential error, we felt it was important to use this more inclusive estimate of the upstream limit rather than the estimate for perennial streams. In addition, we used the elevation limit of intermittent streams because trout in these systems commonly use stream reaches that are seasonally intermittent (J. Dunham, personal observations). We implemented a similar process for evaluating downstream constraints based on the minimum catchment elevation for fish-bearing streams, where terminal basin elevations represented the minimum potential downstream elevation limit. In this case, we plotted the 5th quantile regression versus terminal basin elevation to determine whether downstream limits matched terminal basin elevations (slope = 1), suggesting a topographic constraint, or if they were different from a slope of 1, suggesting that something other than topography limits downstream distributions. The upstream and downstream limits relative to maximum stream elevation and terminal basin elevations were considered separately from the bioclimatic envelope edges because both elevations were correlated and, therefore, they could not be included in a single multiple regression analysis. In evaluating trends in upstream and downstream limits separately, we focused first on upstream limits where steeper gradients and barriers rather than climatic factors typically limit fish distributions.

*Evaluating potential impacts of climate change on habitat availability.*—Overall, the central and western USA are expected to become warmer and drier with reduced snowpack in the coming century (Kapnick and Hall 2012). However, specific, down-scaled climate models that predict local or regional changes in climate are difficult to resolve in our topographically diverse study area (and indeed across most mountainous regions: Daly et al. 2010). Given these uncertainties, rather than test the effects of a specific, down-scaled climate scenario for trout in the northwestern Great Basin, we adopted what has

been termed a scenario-neutral approach (Wilby et al. 2010). Rather than using a specific climate scenario, we assessed a range of potential elevation shifts in the bioclimatic envelope of each trout species (50, 100, 200, and 400 m). Because the bioclimatic envelope for each species changes with latitude, we evaluated shifts separately for low and high latitudes. In order to estimate the potential number of stream kilometers lost from an upstream shift in the elevation limit of a given bioclimatic envelope, we first separated each basin into bins that included 10% of the total elevation relief. We then calculated the mean gradient of streams in each elevation interval over the entire range of elevations in each basin. We then used the mean gradient at each relative location (10% bin) along the stream profile to estimate the number of linear meters of stream occurring over a single meter increase in stream elevation for that bin along the stream profile (Figure 2). Finally, we used our earlier quantile regression results to estimate upper and lower elevation limits for fish

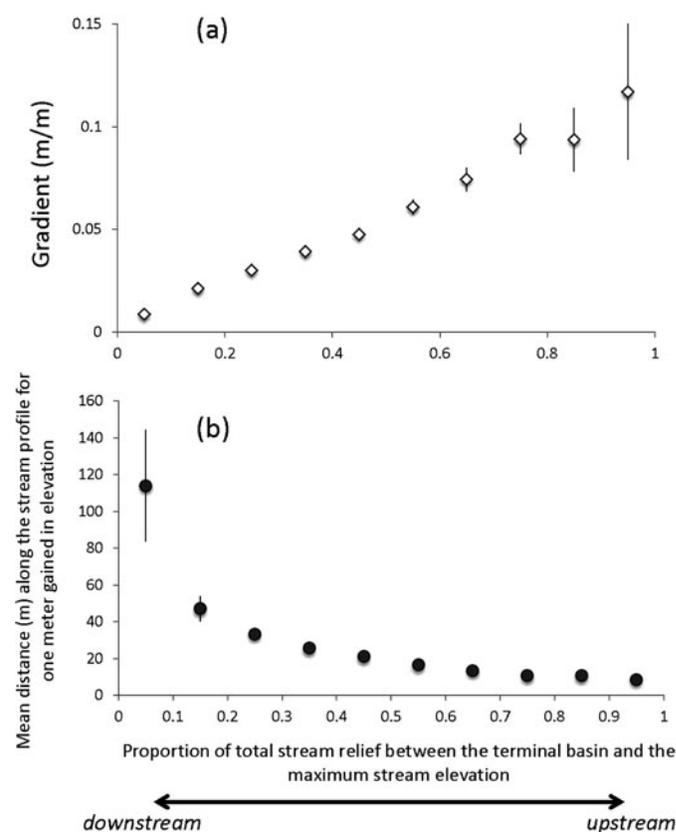


FIGURE 2. Basin-wide trends in gradient and associated stream distance for each meter of elevation gain along a profile of relative stream location from downstream. The proportion of total stream relief between the terminal basin and the maximum stream elevation was binned in 10% intervals, in which 0–0.1 represented the lower 10% of the elevation range of a basin and the 0.9–1.0 bin represented the upper 90% of the elevation range of a basin. Panel (a) indicates mean gradient in a 100-m reach centered on the study site for all study sites within each of 10 proportional intervals of the total relative stream relief, and panel (b) indicates mean linear distance of stream per one meter of elevation gain for all study reaches within a given 0.1 proportional bin of the total stream relief. Bars represent two SEs.

at a given degree of latitude within each species range. Using mean stream gradient at the estimated upstream and downstream elevation limits and the associated linear stream distances for a 1-m gain in elevation, we used simple geometry to estimate the total linear distances of stream habitat that would be likely to be lost or gained at a given location assuming the full climate envelope (both upstream and downstream limits) increased by 50, 100, 200, and 400 m in elevation. In the initial assessment of potential shifts in the bioclimatic envelope, we assumed that the entire elevation envelope could move; however, the assessment of upper quantiles relative to maximum stream elevations suggested that most trout in our study region have likely reached an upstream topographic limit. We therefore also evaluated potential losses associated with a shift in elevations of downstream

limits with no change upstream. If these fish already occur as far upstream as they can, limited upstream movement may be more realistic.

## RESULTS

### Delineation of Bioclimatic Envelopes

Overall, as expected, latitude was a significant factor accounting for variability in both the upstream and downstream elevation limits of all four trout species (Figure 3; Table 1). Longitude was a significant factor only for Lahontan Cutthroat Trout (upstream distribution limit only) and Brook Trout (upstream distribution limit only), and when significant, exerted less influence than did latitude (Tables 2, 3). The quantile

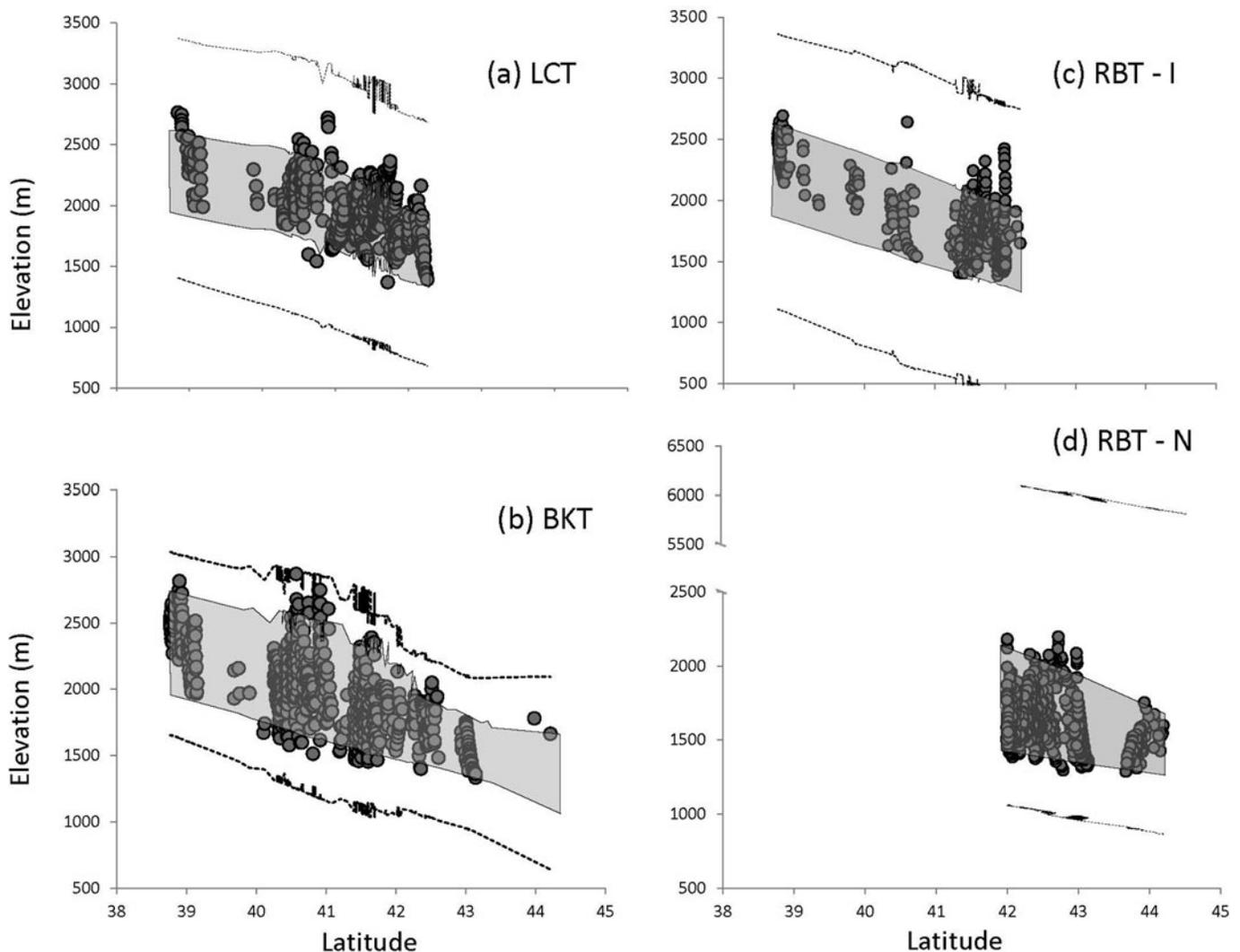


FIGURE 3. Presence of each of four trout species in the northwestern Great Basin as a function of elevation (y-axis) and latitude (x-axis) for each trout species per group of interest: (a) Lahontan Cutthroat Trout (LCT), (b) Brook Trout (BKT), (c) nonnative or introduced rainbow trout (RBT-I), and (d) native Rainbow Trout (RBT-N). The gray box represents the elevation range of the bioclimatic envelope over which 90% of fish observations occurred. The upper and lower edges of this box fall along the 95th and 5th quantiles of the relationship between the elevation of occurrence as a function of both latitude (north-south) and longitude (east-west). High variability at these edges indicates stronger longitudinal influences, whereas low or no variability indicates a limited longitude effect.

TABLE 1. Upper and lower elevation limits (m) at the northern and southern end (latitude) of the species range within our study system for each trout species as defined by the 95th and 5th quantile relationships between elevation and latitude in the northwestern Great Basin.

Species	Latitude (°N)	Downstream limit, 5th quantile (m)	Upstream limit, 95th quantile (m)	Total relief between 5th and 95th quantiles (m)	Sample size for quantile analysis
Lahontan Cutthroat Trout	38.89	2,124	2,745	621	532
	42.26	1,444	2,118	674	
Brook Trout	38.82	1,935	2,833	897	730
	43.14	1,333	1,896	563	
Rainbow Trout (native)	42.02	1,423	2,111	688	757
	44.18	1,255	1,670	415	
Rainbow Trout (introduced)	38.82	1,883	2,622	739	391
	42.17	1,381	2,016	636	

regression process plots demonstrate that the slopes of the quantile regressions remain comparable throughout the distribution between 5th and 95th quantiles, but the estimates are subject to increasing variability and greater error at the edges between 0 and the 5th quantile and between the 95th and 100th quantiles (Figures A.1–A.4).

The relationship between latitude and the edges of Rainbow Trout distributions differed somewhat between the northern basins where they are native and the Lahontan Basin where they are not native; however, the slopes of the 5th and 95th quantiles were not significantly different between native and nonnative regions (Figure 3; Table 2). At the northern end of our study area (44.13°N), the elevation range of Rainbow Trout distribution limits was relatively small but these distributions

encompassed the greatest proportion of potential stream relief observed in the current study (>73% of the potential elevation range; Table 2; Figure 4). Indeed, Rainbow Trout in their native (northern) range were found farther downstream (even to the terminal basin) and farther upstream (closer to the maximum stream elevation in a basin) than any other species.

As upstream and downstream values from the quantile analysis indicate, the elevation range of Lahontan Cutthroat Trout and Brook Trout overlap almost completely throughout the Lahontan Basin indicating a high degree of realized range overlap across the landscape. At the southern extent of the Lahontan Basin, Lahontan Cutthroat Trout and Brook Trout occupy the same proportion of the elevation profile of the stream (Figure 4). At the northern extent of the Lahontan Basin, Brook

TABLE 2. Parameter estimates for relationships between upstream elevation limits of each trout species in the northwestern Great Basin in relation to latitude and longitude as defined by regression models based on the 95th quantile.

Species	Parameter	Coefficient estimate	SE of estimate	Lower limit of CI	Upper limit of CI	<i>P</i> -value
Lahontan Cutthroat Trout	Intercept	18317.36	1213.2	15935.6	20699.2	<0.0001
	Latitude	-193.4	11.7	-216.3	-170.5	<0.0001
	Longitude	69.0	8.5	52.2	85.7	<0.0001
Brook Trout	Intercept	16641.3	899.0	14876.3	18406.4	<0.0001
	Latitude	-168.4	12.7	-193.3	-143.4	<0.0001
	Longitude	63.1	9.1	45.2	80.9	<0.0001
Rainbow Trout (nonnative)	Intercept	11498.3	3387.0	4848.6	18148.0	0.0008
	Latitude	-188.7	17.9	-223.8	-153.6	<0.0001
	Longitude	13.2	28.5	-42.8	69.2	0.643
Rainbow Trout (native)	Intercept	9129.2	3823.2	1623.5	16635.0	0.0172
	Latitude	-199.4	65.3	-327.7	-71.2	0.0023
	Longitude	-11.3	21.5	-53.5	30.9	0.5989

TABLE 3. Parameter estimates for relationships between downstream elevation limits of each trout species in the northwestern Great Basin in relation to latitude and longitude as defined by regression models based on the 5th quantile.

Species	Parameter	Coefficient estimate	SE of estimate	Lower limit of CI	Upper limit of CI	<i>P</i> -value
Lahontan Cutthroat Trout	Intercept	13937.4	2106.2	9802.2	18072.5	<0.0001
	Latitude	-167.7	38.6	-243.4	-92.0	<0.0001
	Longitude	45.9	25.3	-3.8	95.6	0.071
Brook Trout	Intercept	7047.5	1378.4	4341.4	9753.7	<0.001
	Latitude	-153.5	40.3	-232.6	-74.3	<0.001
	Longitude	-7.5	22.3	-51.3	36.4	0.738
Rainbow Trout (nonnative)	Intercept	7292.1	1680.2	3993.3	10590.9	<0.0001
	Latitude	-167.8	52.5	-270.8	-64.7	0.0015
	Longitude	-9.8	24.6	-58.1	38.5	0.691
Rainbow Trout (native)	Intercept	3842.8	715.1	2438.9	5246.6	<0.0001
	Latitude	-75.1	7.5	-89.7	-60.4	<0.0001
	Longitude	-6.1	5.5	-17.0	4.8	0.272

Trout occupy a slightly greater range, although the differences were not significant (Figure 4).

### Topographic Constraints

The trend in overall proportion of potential stream distance occupied was similar for all four species, with a smaller proportion of potential habitat occupied at lower latitudes and a greater proportion of potential habitat filled at higher latitudes (Figure 4). In evaluating trends in upstream and downstream

limits separately, we focused first on upstream limits where steeper gradients and barriers rather than climatic factors typically limit fish distributions. Slopes of the upper 95th quantile regressions reflecting upstream limits in our analysis were consistently positive, but, contrary to our expectations, slopes were significantly less than one for all four species (Figure 5a). The upstream limit for fish occurred closer to the maximum stream elevation in systems with lower maximum elevations. Even in streams with relatively high upstream limits for trout, fish rarely occurred closer than 200 m to their maximum upstream potential elevation. The slopes of the linear relationship along the 95th quantiles used to estimate the upstream extent of fish relative to maximum stream elevation were not significantly different among the four trout species. Lahontan Cutthroat Trout, Brook Trout and nonnative Rainbow Trout had nearly identical upper limits (Figure 5a; Table 2).

Downstream limits to fish distribution relative to terminal basin elevation were more variable but in all cases the slopes were positive and significant. Native Rainbow Trout had a downstream edge with a slope close to one and a downstream limit that approached the terminal basin elevation itself (given our use of the 5th quantile to define edges it is impossible for the line to occur at the terminal basin; Figure 5b; Table 3). An assessment of specific sites indicated that in a number of these systems fish do occur downstream to the terminal basin itself. In contrast, the relationship between downstream limits and the terminal basin elevation for Brook Trout was significantly greater than one (based on the 95% CIs) indicating that the downstream limit to Brook Trout was substantially higher in streams with higher terminal basins than in those with lower terminal basin elevations (Figure 5b). Nonnative Rainbow Trout had an alternate trend to

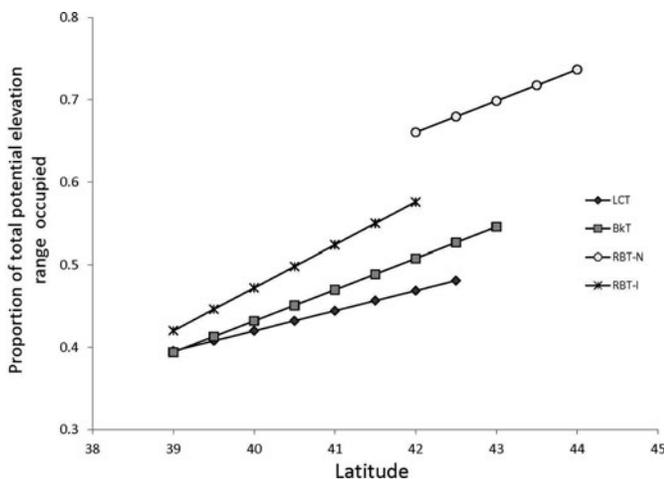


FIGURE 4. The proportion of total elevation relief occupied by each species as a function of latitude. Proportions were calculated by the difference in predicted upstream and downstream limits (95th and 5th quantiles), divided by the total elevation relief. Trout species are abbreviated as follows in the legend: Lahontan Cutthroat Trout, LCT; Brook Trout, BKT; native Rainbow Trout, RBT-N; introduced or nonnative Rainbow Trout, RBT-I.

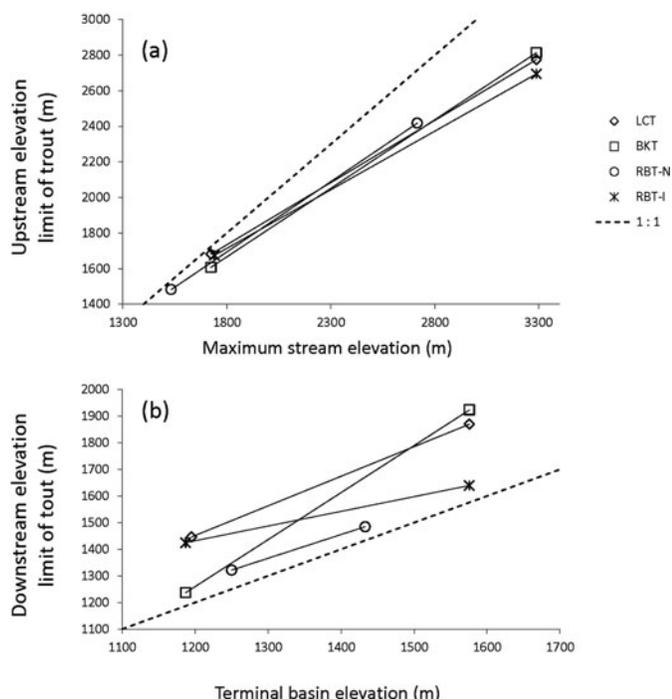


FIGURE 5. (a) Upstream distribution limits relative to their maximum upstream potential (maximum stream elevation) as derived from the 95th quantile regression for all four trout species. (b) Downstream distribution limits relative to their terminal basin elevation as derived from the 5th quantile regression for all four trout species. Trout species are abbreviated as follows in the figure: Lahontan Cutthroat Trout, LCT; Brook Trout, BKT; native Rainbow Trout, RBT-N; introduced or nonnative Rainbow Trout, RBT-I.

that of Brook Trout, with fish occurring closer to the terminal basin in high elevation sites than in low elevation sites.

### Potential Impacts of Climate Change on Habitat Availability

Due to the nature of stream gradient profiles in our study region, upstream shifts in the envelope of potential occupancy for trout will have a much more severe effect on habitat availability in the north (Figure 6). Brook Trout occur across the greatest range in latitude (when considering native versus nonnative Rainbow Trout separately) and they exhibit the greatest differences in response to a shift in the bioclimatic envelope by latitude. At the southern end of our study area, a 100-m elevation shift upstream in the bioclimatic envelope of Brook Trout leads to a net loss of about 1 km of stream habitat. However, at the northern extent of Brook Trout in our study area, a 100-m shift in the bioclimatic envelope could result in the net loss of as much as 7.3 km of stream (Figure 6). As expected, habitat losses under a fixed upstream limit were notably larger than under a scenario in which the whole envelope shifted upstream.

## DISCUSSION

Our study identified a number of strong gradients in elevation limits for trout in the northwestern Great Basin. Downstream el-

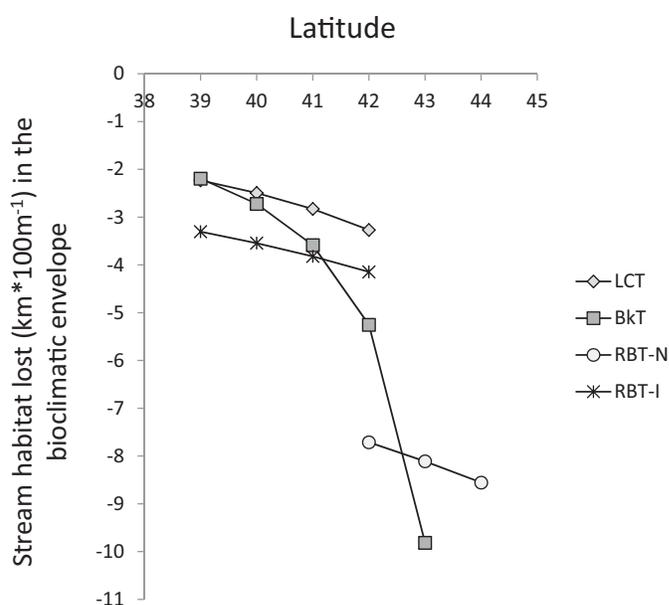


FIGURE 6. Estimated number of kilometers of stream habitat lost given a 100-m upstream shift in the bioclimatic envelope for each trout species assuming only increases in downstream elevation limits. Trout species are abbreviated as follows in the figure: Lahontan Cutthroat Trout, LCT; Brook Trout, BKT; native Rainbow Trout, RBT-N; introduced or nonnative Rainbow Trout, RBT-I.

evaluation limits for trout were well defined and consistent with trends in climate across the region. As expected based on earlier work on fish and other species in this region (Smith 1978; Grayson 1993; Dunham et al. 1999; Rowe et al. 2011), the downstream elevation limits of trout were lower in the north where temperatures are cooler and higher in the south where temperatures are warmer. We also observed a clear latitudinal gradient in upstream elevation limits. The upstream limit of all four trout species was higher in the south than in the north, which is consistent with the trend in maximum mountain height from the north (lower) to the south (higher) in our study region. However, the upstream and downstream limits for trout in the Great Basin are not uniformly limited by geographical or climatic constraints across the region. The realized upstream limits of trout were lower relative to their maximum potential in the south, particularly in the taller mountains where, in addition to steep gradients, stressful winter conditions or an abbreviated growing season could contribute to lower upstream limits (Cunjak 1996; Cole et al. 2006; Coleman and Fausch 2007). Conversely, downstream limits in the northern basins extended all the way to the terminal basin, and thus topography exerted a fundamental constraint to trout distribution.

We found a high degree of overlap in elevation limits of native and nonnative trout in the northwestern Great Basin (native Lahontan Cutthroat Trout, nonnative Brook Trout, and both native and nonnative Rainbow Trout), suggesting there is little opportunity for native trout to find refuge from nonnative trout. We were not able to explore the potential for finer-scale

segregation among species with the available data, but more detailed studies of fish distributions within streams often show evidence of segregation at finer scales (Dunham et al. 2002a, 2002b; Macneale et al. 2010)

Overall, trout occupied a smaller proportion of their total potential elevation range in more southerly latitudes suggesting that reductions in available habitat (e.g., related to climate change or local human impacts) have the potential to further constrain and isolate populations already existing within restricted ranges and limited capacity for interaction. Conversely, when considering vulnerability of trout in terms of the magnitude of potential habitat loss, we found that more northerly populations were most vulnerable. Greater vulnerability for northern populations was related to (1) the strong latitudinal gradients in topographic constraints to upstream elevation limits, particularly the lower mountains in the north leading to lower elevations of potentially suitable streams, and (2) the nature of stream profiles in the north with lower gradients in valley bottoms. In the northern portion of our study area the downstream edge of trout presence regularly occurred in these lower gradient downstream sections, where even slight elevation increases in the downstream limit for trout yielded a substantial loss of linear stream habitat. This highlights the importance of interactions between climate, geography, and topography when considering species distributions and potential effects of climate change or local human influences on suitable habitats (Dunham et al. 1999; Rieman et al. 2006).

In our assessment of upstream limits relative to maximum stream elevation, we found, as expected, that the maximum upstream limits for each species were significantly and positively related to the maximum upstream potential (maximum stream elevation). However, as total mountain elevations increased, upstream distributions limits for trout fell increasingly short of the maximum potential stream elevation. This may be attributed to a greater likelihood of encountering waterfalls, high gradient stream sections, or other factors that limit upstream movement of trout before fish approach maximum stream elevations on increasingly higher mountains (Latterell et al. 2003; Cole et al. 2006; Fransen et al. 2006). Latterell et al. (2003), for example, found that the limit to fish distribution was attributable to steep cascades, step-bed channel profiles, or waterfalls in 68% of unlogged basins and 81% of logged basins. Also, in the eastern United States, Warren et al. (2008) found that the edge of fish distributions could be clearly attributed to waterfalls, cascades, or a lack of water in 68% of the streams surveyed. In addition to physical barriers, the high-elevation streams of Oregon and Nevada have a limited growing season, which may constrain the capacity of higher elevation streams to support fish (Coleman and Fausch 2007).

Given that native Lahontan Cutthroat Trout and native Rainbow Trout have had millennia to colonize stream habitats in the northwestern Great Basin (Behnke 1992; Currens et al. 2009), we feel it is reasonable to assume that farther upstream movement of these species is unlikely, at least without human inter-

vention. As suggested by Buisson et al. (2008) in their analysis of fish distributions in central Europe, shifts in species distributions in response to warming climate conditions will disproportionately impact coldwater species that dominate the headwaters (assuming uniform rates of warming; see Arismendi et al. 2012). These species lose downstream habitat and gain no upstream habitat due to the presence of physical barriers at the upper end of their distributions. The similarity between upstream limits of native trout and the upstream limits of nonnative Rainbow and Brook Trout suggests these nonnative species have colonized the full range of elevations available to them.

Our assessment of potential upstream shifts in the bioclimatic envelope (with both moving and static upper limits) supports the overall conclusion that even slight shifts in stream conditions could substantially reduce available habitat for trout in the northwestern Great Basin. The strong influence of latitude on the amount of potential habitat loss is attributable to northern distribution limits that extend downstream into wide, flat, valley bottoms. Under these conditions, trout in the north stand to lose many more kilometers of river for the same elevation shift in the bioclimatic envelope than do trout in the south (see also Dunham et al. 1999; Rieman et al. 2006). The relationship between latitude and potential habitat loss was particularly striking for nonnative Brook Trout in the northern Great Basin. This relationship is likely due in part to the broader geographic extent of Brook Trout in our study region. Nonnative Brook Trout were present over a large latitudinal range with projected habitat losses in the north that were much more dramatic. These conclusions reflect broad potential responses based on the assumption that warmer terrestrial climates will shift the bioclimatic envelope of trout upstream. Local factors, including influences of terrestrial vegetation and groundwater, may strongly modify actual responses of stream temperatures to changing climates (Acuña and Tockner 2009; Tonolla et al. 2010; Arismendi et al. 2012).

Although we were able to gain many key insights about the distribution of Great Basin trout from the large pool of available data, lack of repeated sampling of sites over time limited our ability to identify trends that may be linked to climate change (e.g., Chen et al. 2011). We also lacked information on movement barriers (human constructed and natural; Fausch et al. 2009), details of species introductions (see also Miller and Alcorn 1945), stream temperatures, discharge, and other instream or riparian variables that could be locally important. Barriers are a clear problem for fish movement and connectivity in this region. Barriers can isolate fish and create smaller populations that are susceptible to local extinctions due to stochastic variability in population size or local disturbances, such as fire, with no opportunity for recolonization (Fausch et al. 2009). In some cases, however, barriers can be useful in isolating populations from invaders and allowing the persistence of native trout in habitat where they would otherwise be extirpated (Peterson et al. 2008a, 2008b). Whereas local factors can drive patterns of fish presence in streams, our modeling approach was focused

on the edges of these distributions (encompassing 90% of the elevations occupied by trout), essentially evaluating maximum and minimum elevation limits across the broad extent of our study area, and not patterns within those limits.

In conclusion, we were able to use simple data on species occurrence with the latitude and longitude of sampling sites to establish bounds on the bioclimatic envelope of two native species of high conservation concern as well as distribution limits of their primary nonnative counterparts in the region. We further established the importance of both local and geographic constraints to the realized elevation limits of trout in our study region, as well as an evaluation of potential responses to changes in these limits. Future work to provide a more structured view of spatial and temporal patterns of variability in fish distributions, as well as local factors influencing them (e.g., stream desiccation, temperature, movement barriers), would provide an important foundation of information for evaluating how fish and stream environments actually respond to the major changes to both that are anticipated in coming decades.

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Appendix: Estimated Parameters by Quantiles

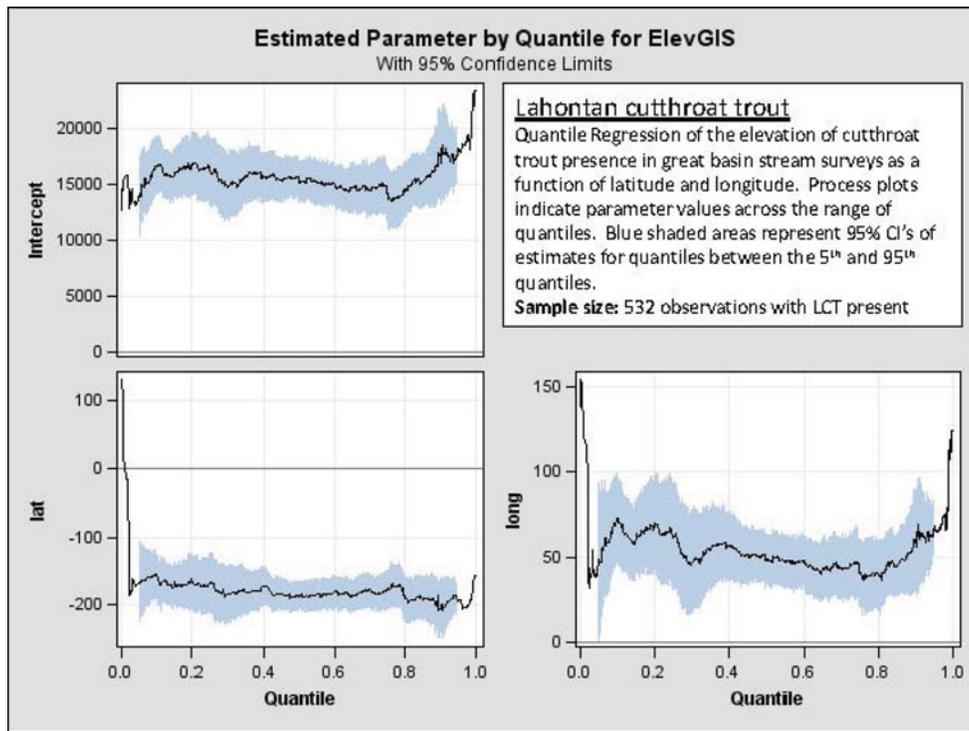


FIGURE A.1. Estimated parameters by quantile for Lahontan Cutthroat Trout.

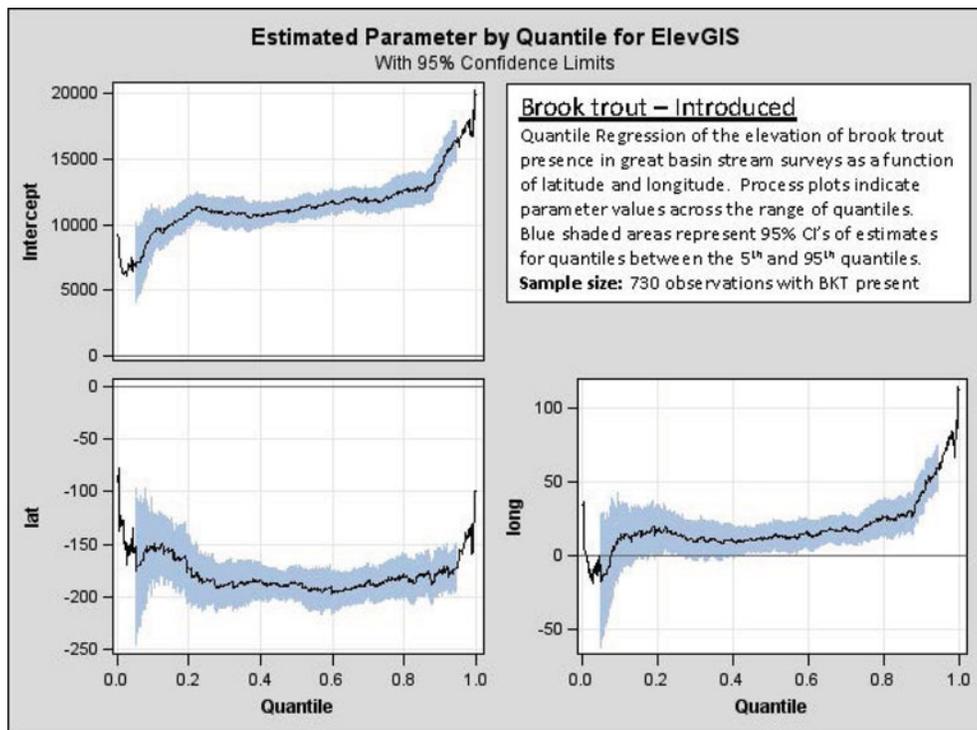


FIGURE A.2. Estimated parameters by quantile for Brook Trout.

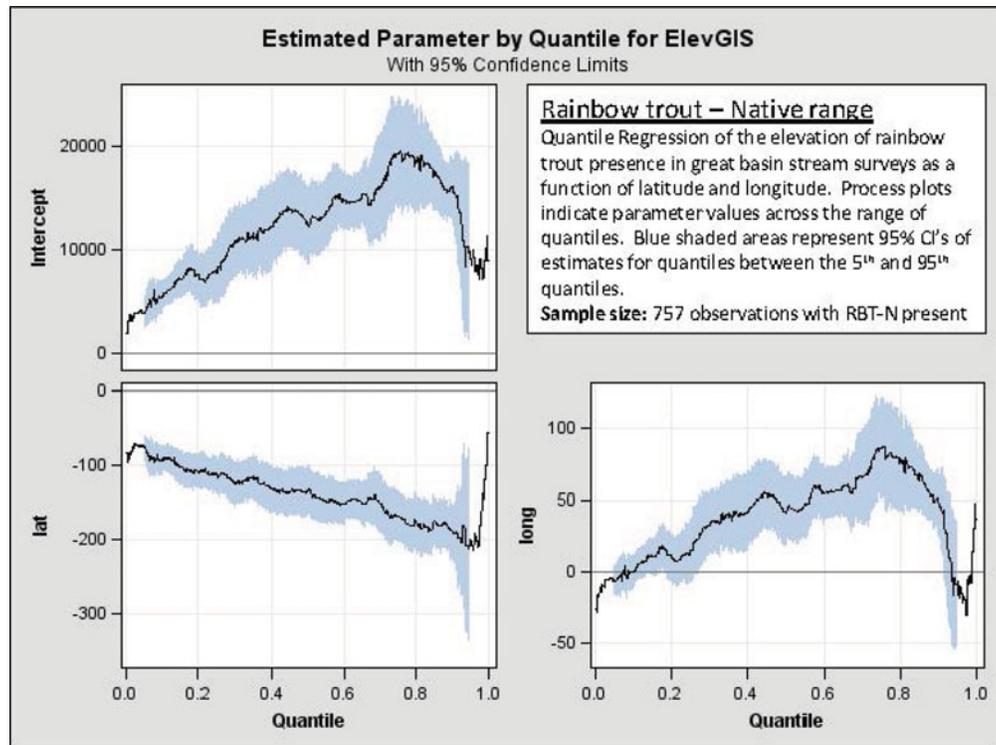


FIGURE A.3. Estimated parameters by quantile for native Rainbow Trout.

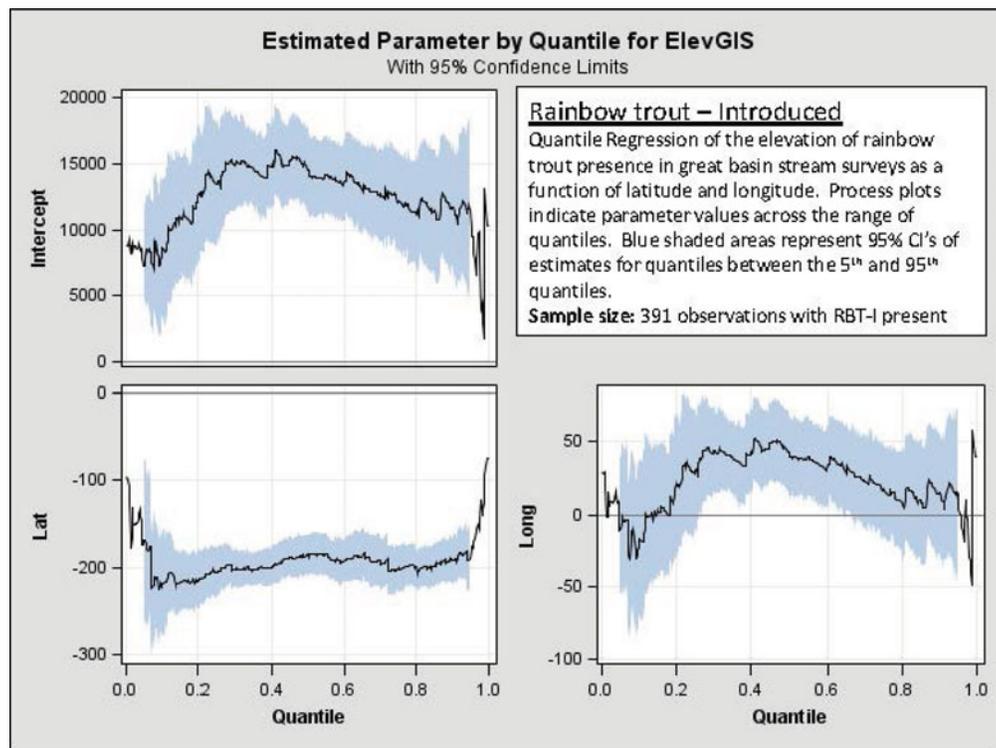


FIGURE A.4. Estimated parameters by quantile for introduced Rainbow Trout.