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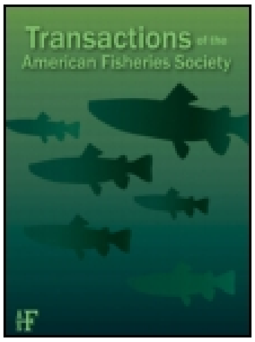

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ARTICLE

Using Aerial Imagery to Characterize Redband Trout Habitat in a Remote Desert Landscape

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Abstract

Remote sensing products, including aerial imagery, can be used to quantify characteristics of watersheds and stream corridors that often predict the distribution and abundance of aquatic species. We conducted a supervised, object-oriented classification of imagery from the National Agricultural Imagery Program to develop a high-resolution (1-m) land cover data set with four cover classes, emphasizing accurate characterization of woody riparian vegetation along stream corridors in northern Nevada and southwestern Idaho. The overall classification accuracy was 76%, and producer's accuracy (reflecting false positives) and user's accuracy (reflecting false negatives) for the woody vegetation class were 84% and 70%, respectively. Using logistic and quantile regression models in a model-selection framework, we found woody vegetation to be positively associated with the occurrence and density of Redband Trout *Oncorhynchus mykiss gairdneri*. In addition, occurrence probabilities and densities were highest at mean August stream temperatures (predicted from a stream temperature model) ranging from 13°C to 17°C. When considered together with stream temperature, percent woody vegetation typically predicted Redband Trout occurrence and density better than most field-measured instream and riparian habitat variables in northern Nevada. Our study highlights how free high-resolution imagery can be used to characterize woody riparian vegetation and Redband Trout habitat across a large and remote desert landscape that can be difficult to access for field surveys. It also suggests that imagery from the National Agricultural Imagery Program may have wider application in identifying stream habitat restoration opportunities, where land and water uses have negatively impacted woody riparian vegetation in desert regions of the interior western United States.

Landscape features, such as watershed land use and valley confinement, influence stream habitat and the distribution and abundance of aquatic organisms, and these features can often be described using remote sensing products (e.g., satellite imagery, thermal imagery, and aerial photography) (Rose et al. 2014; Vatland et al. 2015). For example, the National Land Cover Dataset (Wickham et al. 2013) is derived from Landsat Thematic Mapper satellite imagery and has been widely used to predict fish occurrence and abundance in streams (Hughes et al. 2006; Dauwalter et al. 2011). While useful for characterizing the large features of the landscape, satellite imagery was not designed to characterize small, fine-grained landscape features at high resolutions (10 m or less). In contrast, aerial imagery is one type of remote sensing that is often high resolution (1 m or less), and it is increasingly being used to study fisheries and aquatic ecosystems (Wirth et al. 2012). For example, Booth et al. (2007) found that riparian condition assessments using high-resolution aerial imagery (2-cm resolution) were comparable to ground-based assessments but that the use of aerial imagery was faster and allowed for greater sampling intensity and broader spatial coverage. Aerial imagery has been used to quantify changes in river channel morphology and guide stream restoration (Carpenter et al. 2012; Leglieter 2013; Tamminga et al. 2015), quantify

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abundance of aquatic vegetation in lakes (Valta-Hulkkonen et al. 2005), and assess habitat suitability for wetland species (Shealer and Alexander 2013).

One example of widely used aerial imagery is that produced by the National Agriculture Imagery Program (NAIP) administered by the U.S. Department of Agriculture's Farm Service Agency. The NAIP acquires aerial imagery during the agricultural growing season (i.e., "leaf-on") in the continental USA and makes it freely available to the public within 1 year of acquisition. The imagery is typically 1-m resolution and acquired as a three- or four-band product, with red, green, and blue bands and an optional near-infrared band that allows it to be used as natural color or color infrared images. The horizontal accuracy of NAIP imagery from 2006 and later is required to be within 6 m of true ground at a 95% confidence level. Because of its free availability and high resolution, NAIP imagery is served with many commercial products, such as in Google Earth (www.google.com/earth/). These characteristics make NAIP imagery ideal for characterizing small-scale features of streams, and, in fact, it has been used to delineate and characterize riparian areas (Booth et al. 2012). However, the NAIP has not been widely used in fisheries, which is surprising given its availability and the influence that small-scale stream features, such as riparian vegetation, have on habitats used by stream fishes (Cross et al. 2013; Dauwalter et al. 2014).

The Columbia River Redband Trout *Oncorhynchus mykiss gairdneri* is native to the Columbia and Frazer River basins east of the Cascade Range, where it occupies a variety of habitats ranging from mountain lakes to desert streams (Benke 2002; Muhlfeld et al. 2015). In desert environments, resident Redband Trout occupy small- to medium-sized streams with mean summer (June through August) temperatures less than 20°C (Meyer et al. 2010) and they mature in the first or second year of life (Schill et al. 2010; Meyer et al. 2014). The extent of habitat occupied expands and contracts in conjunction with stream drying due to the annual changes in precipitation and streamflow (Zoellick 1999). Redband Trout are often found in streams shaded by riparian vegetation. Zoellick and Cade (2006) found stream shading to predict Redband Trout density slightly better than a composite instream habitat suitability index. They also found the effect of shading on density to be conditional on the distance from stream headwaters—a surrogate for stream temperature—and hypothesized that stream shading from woody riparian vegetation limited, but was not the sole determinant of, Redband Trout densities. While riparian vegetation composition reflects natural gradients in hydrology, nutrients, and other natural factors (Wondzell et al. 2007), it also reflects the intensity of livestock grazing. Grazing has been shown to negatively impact woody riparian vegetation in desert Redband Trout streams, which can result in streambank instability, higher concentrations of fine sediments, and greater insolation and warmer stream temperatures (Li et al. 1994; Zoellick 2004).

Our goal was to evaluate the use of a supervised, object-oriented classification of NAIP imagery to accurately characterize woody riparian vegetation as a tool for characterizing Redband Trout habitat and predicting the distribution (occurrence) and density of the species in high-desert basins in northern Nevada and southwestern Idaho. Our specific objectives were to (1) develop a high-resolution land cover map from NAIP imagery, with a focus on accurate classification of woody vegetation near streams, (2) evaluate the ability of woody riparian vegetation to predict the distribution (occurrence) and density of Redband Trout, in addition to stream temperature, which is well known to influence the species' distribution, and (3) compare the predictive ability of woody vegetation and stream temperature—both spatially explicit data sets available for mapping and spatial analysis—to field-measured instream and riparian habitat variables at a subset of our study sites. Our study demonstrates how free high-resolution aerial imagery can be helpful in understanding Redband Trout habitat conditions, distribution, and abundance in streams across a high-desert region that is remote and often difficult to access for field surveys.

METHODS

Study Area

Our study area encompassed the upper Salmon Falls Creek and Owyhee River basins in northern Nevada and southwestern Idaho (Figure 1). Both high-desert basins include populations of Redband Trout (Muhlfeld et al. 2015) and have varied topography (elevation range = 665–3,100 m), including deep canyons that are often remote and difficult to access. Climate is characterized by warm summers (mean daily summer temperature range = 10–25°C) and cool winters (mean daily winter temperature range: −20°C to +5°C). Precipitation falls primarily as snow in winter and totals 17–115 cm annually, supporting sagebrush steppe (big sagebrush *Artemisia tridentata* and grasses in the family Poaceae) and juniper *Juniperus* spp. woodland vegetation communities at low elevations and conifer (family Pinaceae) and aspen *Populus* spp. at high elevations. The primary anthropogenic land use in the region is cattle grazing, with surface-irrigated hay pasture as a secondary use.

Supervised NAIP Image Classification

We acquired 1-m-resolution, four-band NAIP imagery to develop a 1-m-resolution land cover data set for our two study basins. Because NAIP data are collected on a state-by-state basis periodically over time, the data we acquired were the most recent at the time of classification and were within a few

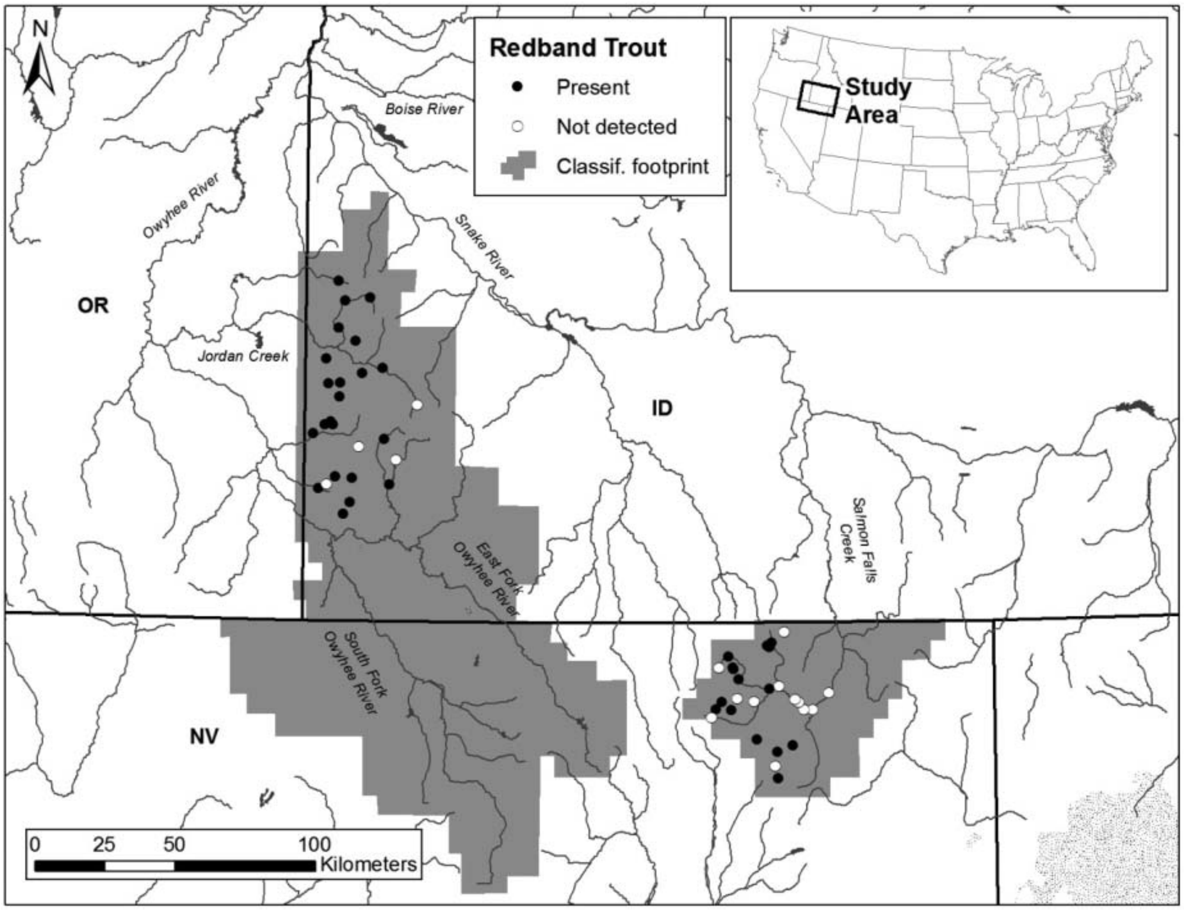

FIGURE 1. National Agricultural Imagery Program (NAIP) classification footprint (gray area) and fish sampling locations (black and white circles) in the Salmon Falls Creek and Owyhee River basins in Nevada and Idaho. Only larger streams and rivers are shown for context; classif = classification.

years of fish survey data (see below): 2010 for Salmon Falls Creek in Nevada, 2006 for the Owyhee River basin in Nevada, and primarily 2009 for the Owyhee River basin in Idaho. We classified the NAIP imagery using a supervised, object-oriented classification into four land cover classes: bare ground, herbaceous riparian vegetation, upland vegetation, and woody vegetation (Table 1). Although our primary focus was on the accurate characterization of woody vegetation along stream corridors, the use of four cover classes helped to distinguish the statistical signature of woody vegetation relative to other classes and improved classification accuracy. Supervised, object-oriented image classification develops unique statistical signatures of each object class based on the size, shape, orientation, texture, and context of pixel values in a neighborhood from multiple image bands that allows differentiation into categorical groupings (Lillesand and Kiefer 2000; Blaschke 2010). The supervised classification was conducted separately for each NAIP image tile (3.75 × 3.75 min quarter quadrangle buffered by 300 m); 90 tiles were classified for Salmon Falls Creek, and 235 were classified for the Owyhee River. To train the classification of each tile, one person, hereafter referred to as "user," digitized five or more polygons (mean size = 0.5 ha; SD = 2.0 ha) around areas that represented each of the four land cover types; all training data were constrained to be in or near floodplain areas (identified using threshold values when multiplying distance from stream by terrain slope). Training data were used to develop the statistical signature for each land cover class that was then used to classify each image tile using Manhattan input representation (diamond-shaped neighborhood) with a neighborhood size of nine cells. The classification output was aggregated (i.e., smoothed) to a minimum feature size of four pixels (i.e., 4 m^2). The supervised classification was implemented using the Feature Analyst extension (Textron Systems, Providence, Rhode Island) within ArcGIS version 10.0 software (ESRI, Redlands, California). Final classifications for each image tile were mosaicked into one land cover raster data set. While the minimum feature size identified in the classification was 4 m^2, we retained the native resolution of the NAIP imagery in the final land cover data set (1 m^2). Images could not be mosaicked and classified all at once due to computational limits and time-of-day and seasonal differences in NAIP flights that resulted in unique differences

TABLE 1. Land cover types identified during a supervised, object-oriented classification of imagery from the NAIP.

Land cover class	Description and key characteristics in aerial photographs
Bare ground	Unvegetated areas including roads, rock, and sand and gravel bars.
Herbaceous riparian vegetation	Grasses, forbs, and sedges growing in areas that are seasonally inundated with high flows or influenced by an elevated water table in the riparian zone or near springs or seeps. Characterized by uniform, short vegetation height and high greenness. Pattern is clustered and continuous.
Woody vegetation	Willow (*Salix* spp.), cottonwood (*Populus* spp.), dogwood (*Cornus* spp.), and other woody shrubs and trees in the riparian zone, and aspen (*P. tremuloides*), juniper (*Juniperus* spp.), and subalpine and Douglas fir (*Abies lasiocarpa* and *Pseudotsuga menziesii*) in the uplands. Characterized by vertical structure, as indicated by shading in imagery and robust, leafy growth (high greenness). Pattern is often clustered and continuous.
Upland vegetation	Includes a continuum of upland vegetation ranging from grasses (cheatgrass [*Bromus tectorum*], native bunchgrasses [Poaceae]) to sagebrush [*Artemisia* spp.] to deciduous shrubs (serviceberry [*Amelanchier* spp.], chokecherry [*Prunus* spp.]). Characterized by low to moderate greenness and a clustered and continuous pattern.

in the multiband statistical signatures of each cover class in each image.

The classification accuracy of our final land cover data set was assessed by using an error matrix (Lillesand and Kiefer 2000). The error matrix was created by (1) generating at least 25 random points at least 200 m apart in floodplain areas within each land cover class, (2) attributing each point with the class value, and (3) having a second user (here considered as reference or truth) independently attribute each point to one of the four land cover classes by visual interpretation of NAIP imagery (Cleve et al. 2008). Visual interpretation was occasionally supplemented with Bing imagery (0.3-m resolution from mid-July 2010; Microsoft Corporation) when land cover in NAIP images was unclear. All imagery was viewed by the user at a 1:1,500 map scale. The error matrix was used to compute the producer's and user's accuracy for each land cover type. The producer's accuracy is computed as the percent of land cover types identified by a user in the imagery that are classified as such by the supervised classification and reflects errors of commission (false positives). The user's accuracy is computed as the percent of land cover types from the supervised classification that are identified as such by an observer viewing the imagery and reflects errors of omission (false negatives).

Redband Trout, Woody Riparian Vegetation, and Stream Temperature

Woody vegetation and stream temperature.—We evaluated the ability of woody vegetation from our NAIP image classification, in addition to stream temperature from a spatially explicit stream temperature model, to predict the distribution (occurrence) and density of Redband Trout by using logistic and quantile regression models in a model selection framework. Woody vegetation was summarized as a percentage of raster cells within a 5-m buffer of the National Hydrography Dataset (1:24,000 scale) stream segments for 200 m upstream and downstream of each sample site (Figure 2). Hereafter we refer to this measure as percent woody vegetation. Mean August stream temperatures (°C) were obtained as spatially explicit predictions from two stream temperature models developed from our study area (Isaak et al. 2010). While we provide a cursory overview of the stream temperature models here, substantial detail on them can be found on the NorWeST website (http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html) and in related publications (Ver Hoef et al. 2006; Isaak et al. 2015). The temperature models we used were fit using spatial statistical models for stream networks (Ver Hoef et al. 2006; Isaak et al. 2010; Isaak et al. 2015). The response variable in the models was mean August stream temperature from tens of thousands of summer stream temperatures measured in the field, and stream temperature was predicted by several GIS-derived geomorphic, hydrologic, and climatic covariates. Covariates included the following: elevation, percent canopy cover (mean percent underlying 1-km stream segment; National Land Cover Dataset, 30-m resolution), stream slope, drainage area, latitude, proximity to lakes, base flow index values (Wolock 2003), and presence of a tailwater below a dam, which are all static in time. The two temporally varying predictors (by year) were mean August air temperature and mean August streamflows, which allow for predictions under future climates. The models predict mean August stream temperature for each year from 1993 to 2011, including 1993–2011 averages. Because the covariates are GIS-derived predictors, mean August stream temperatures are predicted at the spatial grain of 1-km stream segments for all streams within each modeling domain. We used temperature predictions from two separate models: an Upper Snake–Bear River model that included Salmon Falls Creek (root mean square prediction error [RMSPE] = 1.47°C; r^2 = 0.86) and a mid-Snake River model that included the Owyhee River basin (RMSPE = 1.06°C; r^2 = 0.92). The 1993–2011 average mean August stream temperature for the stream segment on which

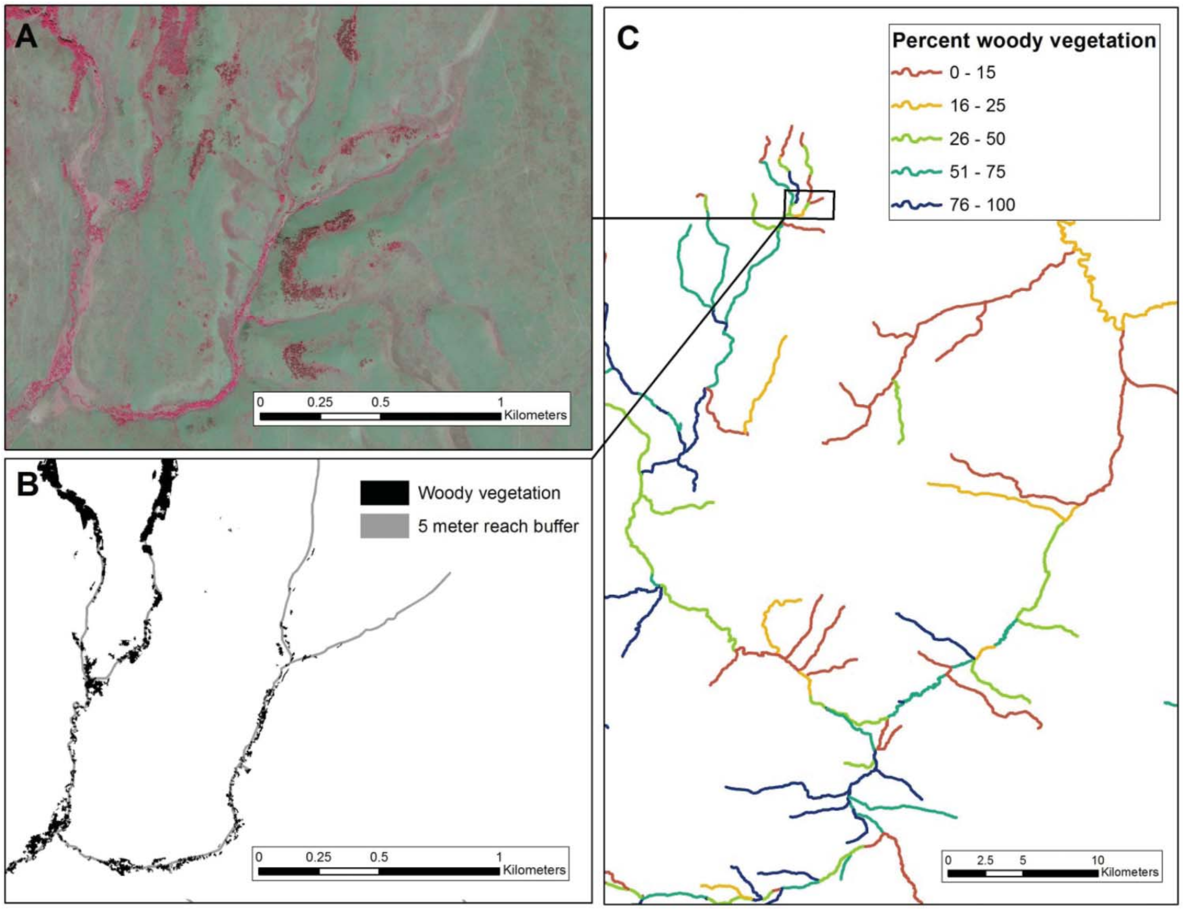

FIGURE 2. Example of **(A)** original NAIP imagery that was **(B)** classified as woody vegetation using object-oriented, supervised classification and then **(C)** summarized as percent woody vegetation within a 5-m stream buffer.

our field sites occurred was used to represent stream temperature at each site; we could not use year-specific temperature predictions because model predictions were not available for 2013 and 2014 when many of our field sites were sampled.

Fish sampling.—From 2008 to 2014, 52 stream sites were sampled for salmonids in the Salmon Falls Creek and Owyhee River basins (Figure 1); the 27 sites in Salmon Falls Creek were sampled from 2013 to 2014, and the 25 sites in the Owyhee Basin were sampled from 2008 to 2010 (Kozfkay et al. 2010; Butts et al. 2011). Nineteen sites in Salmon Falls Creek (in Nevada) were originally selected for sampling based on a generalized random tessellation stratified (GRTS) sampling design (a spatially distributed design stratified by stream order) used for a Redband Trout survey by the Idaho Department of Fish and Game in 2003 (Meyer et al. 2014); however, six sites could not be sampled because access was denied by landowners. We sampled an additional 14 sites to sample Redband Trout populations identified during a recent species rangewide status assessment (Muhlfeld et al. 2015) that were not encompassed by the GRTS design, to maximize spatial coverage in the watershed (in Nevada), to represent the range of stream habitat conditions in the watershed, and to increase sample size; sites sampled on populations occupying an interconnected drainage network were located on unique tributaries as to minimize any potential effect of spatial autocorrelation in our data. In the Owyhee Basin, sites were sampled as part of a long-term monitoring program for Redband Trout by the Idaho Department of Fish and Game for which sites were selected because they were previously found to be occupied by Redband Trout (Zoellick et al. 2005; Kozfkay et al. 2010; Butts et al. 2011).

Salmonids were sampled at each site in a reach, which was typically 100 m in length (thalweg; range = 50–165 m), and isolated with block nets or natural impassable features, such as beaver dams. Fish were sampled with multiple-pass electrofishing using one or two Smith-Root LR-24 or 15-B backpack electrofishers and two- to four-person crews and by visual observation (one person) at one site. We used visual observation to estimate abundance at one intermittent reach, where fish were congregated into two small pools and were thought to be thermally stressed. Fish were easily identified and the total length of counted individuals was estimated. After fish sampling at the 27 Salmon Falls Creek sites, we assessed instream habitat, streambank conditions, and riparian vegetation using transect-based sampling and U.S. Bureau of Land Management Multiple Indicator Monitoring (Burton et al. 2011) measures of riparian condition. At each site, 10 transects were established every 10 m along the reach beginning at the downstream reach boundary. Transects were placed across the stream channel at bank-full height, which was identified based on the height of depositional surfaces, the presence of perennial vegetation, topographic breaks, bank substrates, undercut banks, and water stain lines (Harrelson et al. 1994; Burton et al. 2011). Channel depth, wetted width, water depth, stream substrate, and cover were recorded at 10 equidistant points along each transect (Platts et al. 1983). Stream substratum at each point was classified according to the modified Wentworth scale as follows: bedrock, silt or clay (<0.064 mm in diameter on *b*-axis), sand (0.064–2.000 mm), gravel (2–15 mm), pebble (15–64 mm), cobble (64–256 mm), and boulder (>256 mm) (Cummins 1962). Cover was classified as follows: boulder, large wood (>10 cm in diameter, >4 m in length), submergent vegetation (aquatic macrophytes), overhanging bank vegetation, and undercut bank (>10 cm in depth). The surface water elevation difference between upstream and downstream reach boundaries was measured using a survey level and stadia rod, and stream slope was computed as the elevation difference divided by thalweg length (expressed as a percentage). Residual pool depth was measured as maximum pool depth minus water depth at the downstream riffle crest for all pools identified using the classification of Hawkins et al. (1993). Woody vegetation height was classified directly above each transect endpoint at the channel margin as 0.0–0.5 m, 0.5–1.0 m, 1.0–2.0 m, 2.0–4.0 m, 4.0–8.0 m, and > 8.0 m (Burton et al. 2011). Streambank stability was classified at each transect between the water's edge and bank-full height as follows: fracture, slump, slough, eroding, or absent (Burton et al. 2011). At all sites, reach area was computed as reach length multiplied by the mean of multiple wetted width measurements.

At all sites the abundance of Redband Trout was estimated using the Zippin removal method (Zippin 1958) as implemented in the FSA package in Program R (Ogle 2013; R Core Team 2015); to reduce potential bias due to size-dependent capture efficiency the estimates were done separately for fish < 100 mm TL and ≥ 100 mm TL and then summed. The visual count was divided by a 0.8 detection probability as an estimate of abundance (Bozek and Rahel 1991). The density of Redband Trout was expressed as the number of individuals per 100 m^2, which was computed by dividing the abundance estimate by the wetted reach area multiplied by 100. The density of Brown Trout *Salmo trutta* greater than 100 mm TL (number/100 m^2) was also evaluated as a biotic measure of local habitat that could influence Redband Trout density through predation of small individuals.

Redband Trout occurrence.—We evaluated the ability of percent woody vegetation and mean August stream temperature to predict Redband Trout occurrence using logistic regression models within a model selection framework. Our global model included four predictor variables: percent woody vegetation, mean August stream temperature, a quadratic temperature term, and an interaction term between percent woody vegetation and temperature (main effect term only). The response variable was Redband Trout presence (1) or absence (0) at a stream site. This global model was based on past research showing that the effect of woody vegetation on Redband Trout was conditional on stream temperature (i.e., a woody vegetation × temperature interaction; Zoellick and Cade 2006) and that Redband Trout typically do not occupy very cold or warm streams (thus requiring a quadratic term; Meyer et al. 2010). In addition to the global model, two additional candidate models were evaluated based on a subset of terms in the global model. The first candidate model included both the temperature main effect and quadratic terms and percent woody vegetation but did not include the temperature × percent woody vegetation interaction. The second model only included the two temperature terms. Because salmonids are known coldwater stenotherms and their distribution has repeatedly been shown to be influenced by temperature (Zoellick 1999; Meyer et al. 2010; Wenger et al. 2011), we included both temperature terms in all candidate models not to evaluate whether temperature is important to Redband Trout but rather to estimate its effect size in our data (Johnson 1999; Arnold 2010). Akaike information criterion adjusted for small sample size (AIC$_c$) was used to evaluate the plausibility of all candidate models; the model with the lowest AIC$_c$ value was considered the most plausible. Akaike weights were computed as a measure of the probability that the model is the correct model for models within 4 AIC$_c$ units (ΔAIC$_c$) of the best model (i.e., plausible models; Burnham and Anderson 2002). If multiple models were plausible (ΔAIC$_c$ < 4), then model averaging was performed with shrinkage (Lukacs et al. 2010) and Akaike weights to estimate parameters and standard errors based on model selection and parameter uncertainty. Model fit was evaluated with a Hosmer–Lemeshow test with 10 groups (g = 10; Hosmer and Lemeshow 2000). Predictive performance was evaluated using a fivefold, cross-validated area under the curve (AUC) of a receiver operating characteristic plot, where values of 0.5 indicate no discrimination (predictive ability) and values of 1.0 indicate complete model discrimination (Hosmer and Lemeshow 2000). Logistic regression models were fit using the glm function with a logit link in Program R (R Core Team 2015).

Redband Trout density.—We also evaluated percent woody vegetation, in addition to mean August stream temperature, as a predictor of Redband Trout density (number/100 m^2) using quantile regression (Cade and Noon 2003). Modeling the quantiles of a response variable distribution, as opposed to the mean response typically modeled in regression analysis, can be more informative for understanding ecological processes. When upper quantiles are modeled they effectively represent the potential maximum response to one or more variables at different levels of those variables and thus can be viewed as an evaluation of limiting factors (Cade and Noon 2003). As before, our global quantile regression model included four variables: percent woody vegetation, mean August stream temperature, a quadratic temperature term, and an interaction term between percent woody vegetation and temperature. Candidate models were the same two subsets of the global used for occurrence modeling. All quantile regression models were fit to the 90th percentile (0.9 quantile) of the response variable, which was the $\log_e$ transformed Redband Trout density (all sizes; Redband Trout/100 $m^2 + 1$). Models were fit using the quantreg package (Koenker 2013) in Program R (R Core Team 2015), parameter standard errors were estimated using the xy-bootstrap method, and models were evaluated using the AIC_c statistic developed for quantile regression: $rqAIC_c$ (Cade et al. 2005). As before, the model with the minimum $rqAIC_c$ was considered the most plausible, and models within < 4 $rqAIC_c$ units were considered plausible as well. If needed, model averaging was done using shrinkage and Akaike weights. Model fit was evaluated using the quantile coefficient of determination (R^1), which represents the proportional reduction in objective function by a model when compared to an intercept-only model (Cade et al. 2005).

Comparisons with Field Data

We compared the ability of percent woody vegetation as classified from NAIP imagery to predict Redband Trout occurrence and density to that of field-measured instream and riparian habitat. We did so by comparing a broader set of candidate models that included field-measured habitat variables at 27 sites in Salmon Falls Creek. Prior to developing candidate models and performing model selection, we used Spearman rank correlations to identify and remove highly correlated habitat variables ($r_s > 0.7$) from consideration in competing models and used a principal components analysis to visualize interrelationships among field habitat variables, percent woody vegetation, and stream temperature. We used a model selection framework to identify the most plausible models from a candidate set that included the candidate models with percent woody vegetation used previously, candidate models with both temperature terms (linear and quadratic) and one of the field-measured habitat variables, or models with only field-measured habitat variables. However, since detailed habitat assessments were only collected in Salmon Falls Creek and, thus, our sample size was limited to only 27 sites, we constrained our candidate models to have only three predictor variables to keep our sample size to variable ratio near 10:1; our one exception was that we also fit our global model (with the woody vegetation × temperature interaction term) that was used in previous analyses because of the importance of that model as shown by previous research (Zoellick and Cade 2006). Model selection statistics and Akaike weights were used to assess the plausibility of candidate models and perform model averaging (with shrinkage) if necessary.

RESULTS

Supervised NAIP Image Classification

In all, 325 NAIP image tiles were classified into four land cover types using the supervised classification. The overall accuracy of the final NAIP imagery-based land cover classification was 76.0% (Table 2). The producer's and user's accuracies were 84% and 70%, respectively, for the woody vegetation class.

Redband Trout, Woody Riparian Vegetation, and Stream Temperature

Redband Trout occurrence.—Redband Trout were collected at 37 of 52 sites (71.2%) in both the Salmon Falls Creek and Owyhee River basins. The logistic regression model with percent woody vegetation and both temperature terms was the most plausible. The global model with the percent woody vegetation × temperature interaction term was also plausible

TABLE 2. Error matrix used to assess the producer's accuracy and user's accuracy of a supervised classification of NAIP imagery into four land cover types. At least 25 random points at least 200 m apart were used to assess the accuracy of each cover type. The values represent the number of points within each classified and observed class type. The producer's accuracy and user's accuracy are defined as a percentage.

Supervised classification, total, and producer's accuracy	User observed					
	Woody	Herbaceous	Upland	Bare	Total	User's accuracy (%)
Woody	21	4	4	1	30	70.0
Herbaceous	4	18	1		23	78.3
Upland		1	34		35	97.1
Bare			16	25	41	61.0
Total	25	23	55	26	129	
Producer's accuracy (%)	84.0	78.3	61.8	96.2		76.0

TABLE 3. Number of parameters (K), log-likelihoods, Akaike information criterion (AIC) values, and Akaike weights (w_i) for candidate logistic and quantile ($\tau = 0.9$) regression models predicting Redband Trout occurrence and density as a function of the covariates in Salmon Falls Creek, Nevada, and the Owyhee River, Idaho. The covariates included mean August temperature (temp; °C) from a spatially explicit stream temperature model and percent woody vegetation from a supervised classification of NAIP imagery. Logistic regression models were compared using Akaike information criterion corrected for small sample size (AIC_c), whereas quantile regression models were compared using the AIC_c statistic developed for quantile regression ($rqAIC_c$). Akaike weights were computed for models where ΔAIC_c or $\Delta rqAIC_c < 4$. Fivefold, cross-validated AUC (logistic) and R^1 (quantile) provide measures of model fit.

Model class	Candidate models	K	Log-likelihood	AIC_c or $rqAIC_c$	ΔAIC_c or $\Delta rqAIC_c$	w_i	AUC or R^1
Logistic	Percent woody vegetation + temp + temp^2	4	−24.798	58.447	0.00	0.767	0.723
	Percent woody vegetation × temp + temp^2	5	−24.764	60.832	2.38	0.233	0.688
	Temp + temp^2	3	−29.619	65.737	7.29		0.589
Quantile$_{\tau=0.9}$	Percent woody vegetation + temp + temp^2	4	−108.864	229.032	0.00	0.464	0.133
	Temp + temp^2	3	−110.436	229.724	0.69	0.328	0.106
	Percent woody vegetation × temp + temp^2	5	−108.381	230.629	1.60	0.209	0.141

($\Delta AIC_c = 2.4$) (Table 3); however, inclusion of the interaction term did not effectively reduce the log-likelihood, suggesting that the interaction term explained very little additional variation in occurrence, the interaction model was obsolete, and the best model was the only plausible model (Arnold 2010). The most plausible model fit the data (Hosmer–Lemeshow test: $\chi^2 = 12.5$, $P = 0.132$) but only had moderate out-of-sample predictive ability (fivefold, cross-validated AUC = 0.723). Parameter estimates and model predictions showed a positive, precise effect of percent woody vegetation and a unimodal and less precise response to temperature that peaked near 15°C (Table 4; Figure 3A, B). The probabilities were lower at both the coldest and warmest mean August temperatures, with less precise probabilities at the warmest temperatures (Figure 3A).

Redband Trout density.—Across all sites where Redband Trout were present, densities averaged 29.1 Redband

TABLE 4. Parameter estimates (b_i) and standard errors (SE) for logistic and quantile ($\tau = 0.9$) regression models predicting Redband Trout occurrence and density, respectively. Models with an asterisk indicate model-averaged parameter estimates and standard errors (averaged with Akaike weights and shrinkage). Summed Akaike weights ($\sum w_i$) convey variable importance.

Basin	Model	Parameter	b_i	SE	$\sum w_i$
Salmon Falls Creek and Owyhee River ($n = 52$)	Logistic	Intercept	−23.189	15.918	1.00
		Temperature (°C)	2.904	2.171	1.00
		Temperature^2	−0.096	0.073	1.00
		Percent woody vegetation	0.040	0.014	1.00
	*Quantile$_{\tau=0.9}$	Intercept	−30.551	5.025	1.00
		Temperature	4.267	1.010	1.00
		Temperature^2	−0.134	0.041	1.00
		Percent woody vegetation	0.039	0.049	0.69
		Woody vegetation × temperature	−0.001	0.003	0.22
Salmon Falls Creek ($n = 27$)	*Logistic	Intercept	−156.564	74.179	1.00
		Temperature	22.550	10.458	1.00
		Temperature^2	−0.803	0.366	1.00
		Percent woody vegetation	0.011	0.019	0.39
	Quantile$_{\tau=0.9}$	Intercept	−44.952	39.430	1.00
		Temperature	6.935	5.188	1.00
		Temperature^2	−0.255	0.170	1.00
		Percent woody vegetation	0.012	0.012	1.00

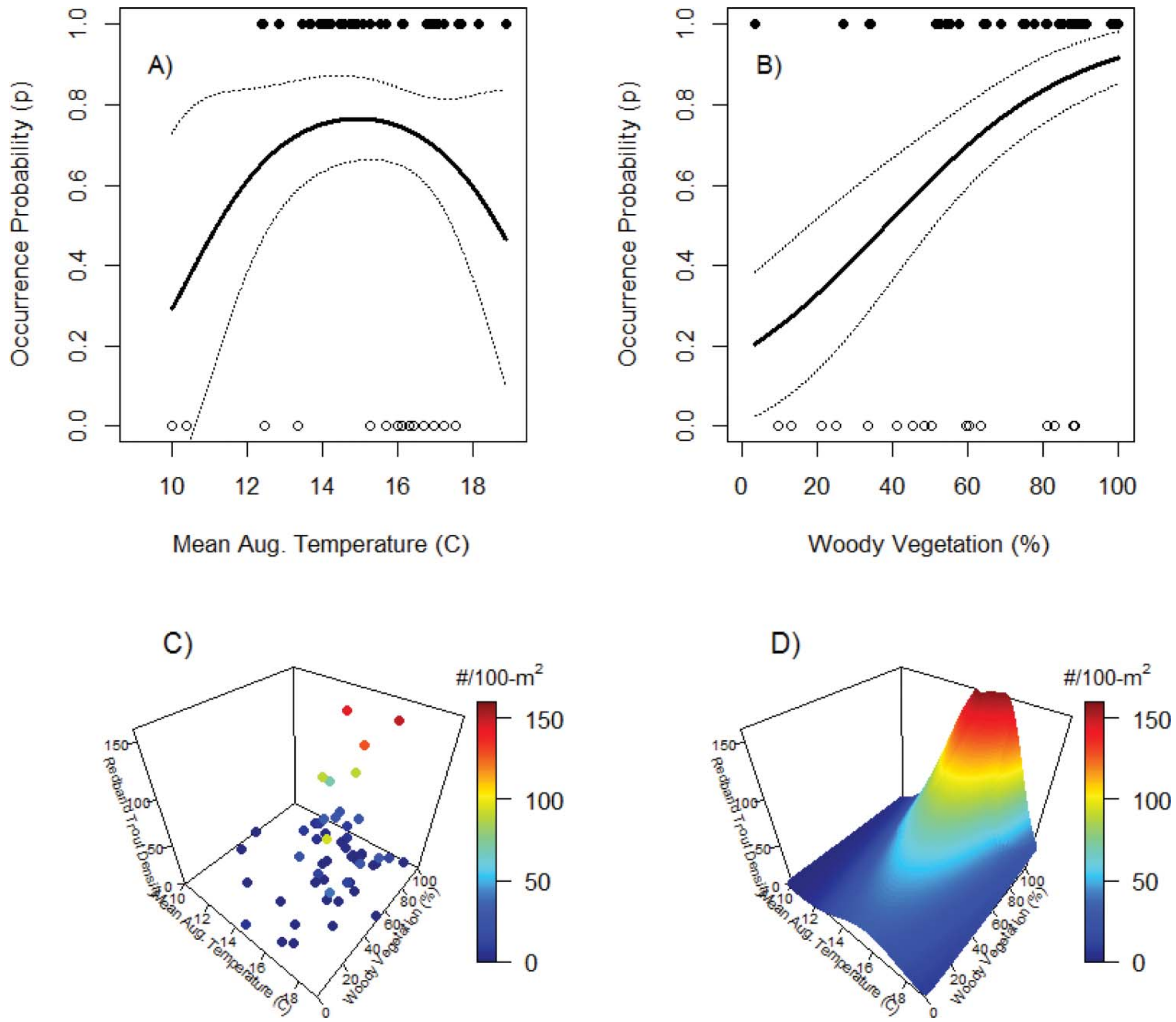

FIGURE 3. Top panels show the predicted Redband Trout occurrence probabilities from a logistic regression model as a function of **(A)** mean August stream temperature and **(B)** the percent of woody vegetation (classified from NAIP imagery) in Salmon Falls Creek and Owyhee River basins combined. The dashed lines represent 90% confidence intervals, and the circles represent observed presences (1; black cirlces) or absences (0; open circles). The bottom panels represent **(C)** the observed Redband Trout density and **(D)** the predicted densities from a quantile ($\tau = 0.9$) regression model as a function of mean August stream temperature and percent woody vegetation in Salmon Falls Creek and Owyhee River basins combined.

Trout/100 m^2 and ranged from 0.3 to 150.5 per 100 m^2 (Figure 3C). While the candidate model with percent woody vegetation and temperature (including the temperature quadratic term) was the most plausible when explaining variation in the 90th percentile of Redband Trout density, all candidate models were plausible (ΔrqAIC$_c \leq 1.60$; Table 3). However, even the most plausible model explained only 13.3% more variance than an intercept-only model ($R^1_{\tau=0.9} = 0.133$; Table 3). The model with only the two temperature terms was the next most plausible model (ΔrqAIC$_c = 0.069$; Table 3). Even the model with the woody vegetation $\times$ temperature interaction was plausible and explained some variation in Redband Trout densities beyond the most plausible model as shown by the reduction in log-likelihood (Table 3). After model averaging, the percent woody vegetation $\times$ temperature interaction parameter estimate was effectively reduced to 0, and the remaining parameter estimates predicted that Redband Trout densities only increased in response to woody vegetation when temperatures were near 15°C (Figure 3D). Although temperature effects were precisely estimated, the parameter estimates for percent woody vegetation were less precise (Table 4).

Comparison with Field Data

Redband Trout were collected at 15 of 27 (55.5%) sites in Salmon Falls Creek, where densities ranged from 0.3 to 69.8 Redband Trout per 100 m^2 when the species was present. Spearman's rank correlations only identified one set of highly correlated habitat variables. Mean wetted width, mean water depth, and residual pool depth were all correlated measures of stream size ($r_s = 0.86$–0.88); we retained residual pool depth as the one measure of stream size from that variable set most likely to influence Redband Trout occurrence and density. Large wood was never observed, root wads were observed at only one site, and these two variables were excluded from any candidate models (Table 5). No other variable pairs had a high enough correlation to meet our screening criterion ($r_s = 0.7$) and so all remaining variables were included in the candidate models. A scree plot from the principal component analysis suggested that the first two principal components explained a majority of the variation among habitat variables; axis 1 explained 30.3% of the variance and axis 2 explained 16.1%. Sites with high scores on axis 1 and low scores on axis 2 represented larger, warm, low-gradient sites, whereas sites with low axis-1 scores and high axis-2 scores represented smaller, cold, high-gradient sites (Figure 4). A second gradient, largely independent of the first gradient, contrasted sites that had more woody riparian vegetation and cobble substrates versus sites

TABLE 5. Summary statistics of habitat variables measured at sites where Redband Trout were present and absent in Salmon Falls Creek, Nevada, in 2013 and 2014 ($n = 27$). Summaries are also given for percent woody vegetation and mean August stream temperature variables for Salmon Falls Creek and Owyhee River basins combined ($n = 52$).

Variable	Redband Trout	Mean	Minimum	Maximum
Woody vegetation (%)	Present	73.4	3.2	98.6
	Absent	47.3	9.5	88.2
Including Owyhee River data	Present	74.2	3.2	100.0
	Absent	48.6	9.5	88.2
Mean August temperature (°C)	Present	14.3	12.4	16.2
	Absent	14.8	10.0	17.2
Including Owyhee River data	Present	15.3	12.4	18.9
	Absent	15.1	10.0	17.5
Slope (%)	Present	2.9	0.3	8.2
	Absent	1.7	0.02	7.2
Mean wetted width (m)[a]	Present	2.53	0.58	7.08
	Absent	5.81	0.37	11.50
Mean water depth (m)[a]	Present	0.11	0.03	0.27
	Absent	0.24	0.02	0.47
Residual pool depth (m)	Present	0.24	0.03	0.89
	Absent	0.56	0.02	1.40
Aquatic vegetation (%)	Present	9.8	0.0	55.8
	Absent	9.5	0.0	52.5
Cobble (%)	Present	21.5	0.0	55.0
	Absent	13.6	0.0	36.4
Fines (silt, clay, sand; %)	Present	18.9	0.0	96.2
	Absent	27.1	1.8	66.7
Small wood (%)	Present	3.0	0.0	16.7
	Absent	5.0	0.0	32.2
Large wood (%)	Present	0.00	0.00	0.00
	Absent	0.00	0.00	0.00
Undercut bank (%)[b]	Present	0.97	0.00	7.50
	Absent	0.17	0.00	2.08
Streambank slough slump (%)	Present	14.3	0.0	40.0
	Absent	17.2	0.0	77.8
Channel width : depth ratio[a]	Present	13.4	5.2	25.2
	Absent	19.1	7.8	37.4
Woody vegetation height (rank: 1–6)	Present	3.4	1.6	5.6
	Absent	2.5	1.2	5.1
Brown Trout (>100 mm TL; number/100 m^2)	Present	0.09	0.00	1.03
	Absent	0.19	0.00	1.36

[a]The variable was not included in the candidate models but is summarized for reference.
[b]The model would not converge when undercut bank was included in the presence–absence models; thus, undercut bank was excluded from the candidate models.

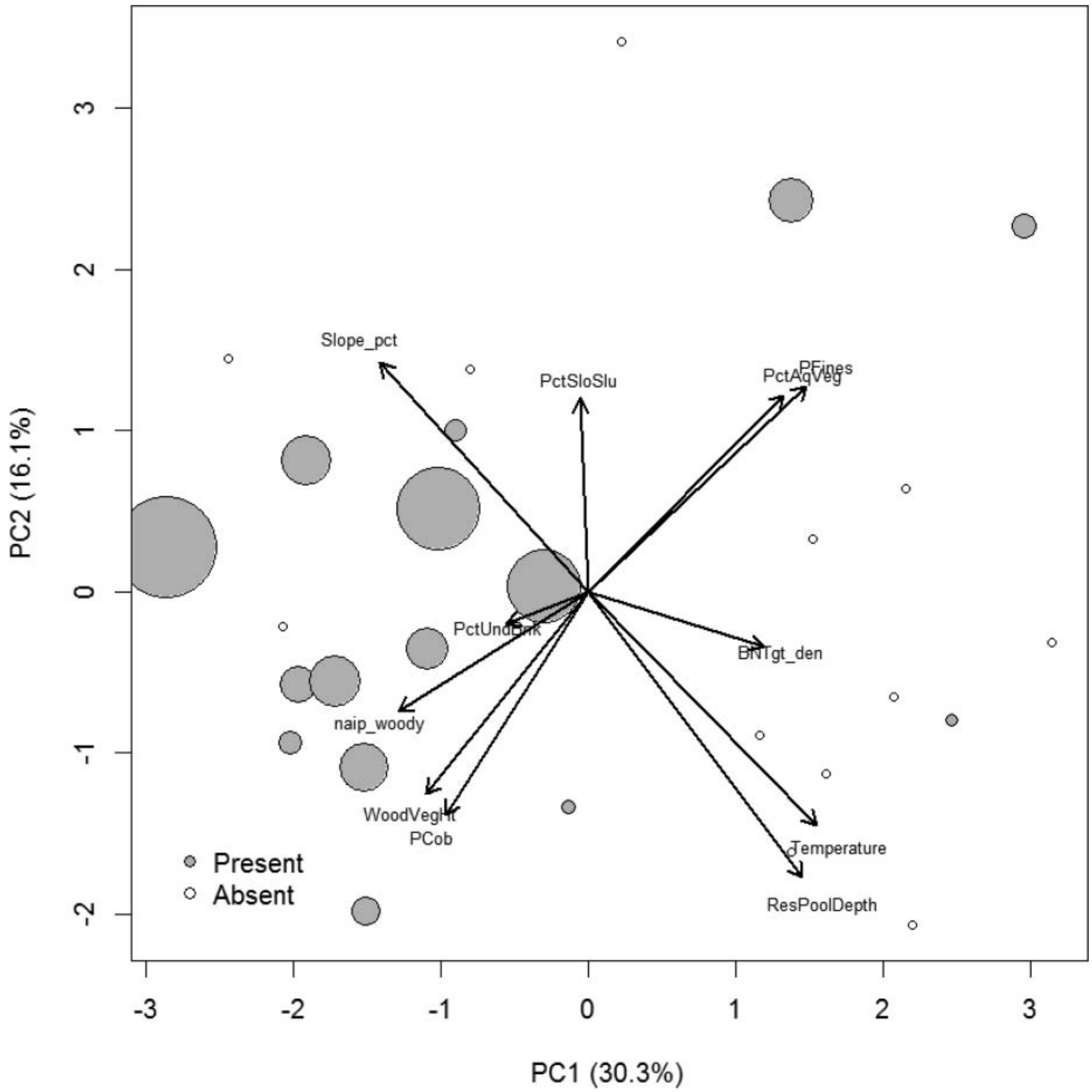

FIGURE 4. Biplot of principal component 1 (PC1) versus principal component 2 (PC2), showing the main habitat gradients and associations among habitat variables in Salmon Falls Creek, Nevada. The percent variance that is explained by each axis is shown in parentheses. The arrows representing the habitat variables are scaled by 4.4 times the loading coefficient. The site locations are shaded by the presence or absence of Redband Trout, and the site symbols are scaled positively by fish density. The variable abbreviations are as follows: naip_woody = percent woody vegetation, Slope_pct = percent stream slope, WoodVegHt = woody vegetation height, PCob = percent cobble, PFines = percent fines (silt, clay, sand), PctAqVeg = percent aquatic vegetation, PctUndBnk = percent undercut bank, ResPoolDepth = residual pool depth, Temperature = mean August stream temperature, and BNTgt_den = Brown Trout greater than 100 mm TL/100 m^2.

with more fine sediment and more aquatic vegetation (Figure 4). Thus, although not strongly correlated, there were general patterns among habitat variables that showed that certain habitat conditions often occurred in concert. When Redband Trout occurrence and density data were overlain on these patterns it was evident that the species most often occurred in sites with moderate temperatures and slopes and with more classified woody vegetation (from NAIP imagery), taller woody vegetation as measured in the field, and more coarse substrates but with a couple of notable exceptions (upper right of the principal component analysis biplot in Figure 4).

Redband Trout occurrence.—Percent woody vegetation and mean August stream temperature predicted Redband Trout occurrence as well as or better than field measures of instream and riparian habitat in the 27 sites surveyed in Salmon Falls Creek. The candidate logistic regression model with only mean August temperature (both linear and quadratic terms) was the most plausible model, and all models with percent woody vegetation ranked highest ($\Delta AIC_c < 4$; Table 6). However, similar to the analysis of the full data set, the candidate model with a percent woody vegetation × temperature interaction explained no additional variation in Redband Trout occurrence than the same model without the interaction term, suggesting very little support for the interaction term (Arnold 2010). All other three-variable models containing the two temperature terms and one field-measured habitat variable were slightly less plausible than the top two models but still plausible nonetheless (Table 6). Models with field-measured habitat only (excluding modeled stream temperature) had no support (Table 6). The most plausible model containing both stream temperature terms and percent woody vegetation fit the data (Hosmer–Lemeshow test: $\chi^2 = 7.55$, $P = 0.479$) and showed good out-of-sample predictive ability (fivefold, cross-validated AUC = 0.83). In fact, almost all plausible models ($\Delta AIC_c \leq 4$) showed good predictive ability (cross-validated AUC > 0.80). Model-averaged parameter estimates for the top two models showed precise temperature effects but an imprecise parameter estimate for percent woody vegetation (Table 5). Occurrence probabilities were highest at mean August stream temperatures near 14.0°C but with a narrower temperature use range than observed across all 52 sites combined (Figure 3A), and probabilities increased with higher percentages of woody vegetation (Figure 5A, B).

TABLE 6. Number of parameters (K), log-likelihoods, Akaike information criterion, and Akaike weights (w_i) for candidate logistic and quantile ($\tau = 0.9$) regression models predicting Redband Trout occurrence and density as a function of covariates in Salmon Falls Creek, Nevada. The covariates included mean August temperature (temp; °C) from a spatially explicit stream temperature model and percent woody vegetation from a supervised classification of NAIP imagery. Field-measured covariates are defined in the Methods section. Logistic regression models were compared using AIC_c (the Akaike information criterion corrected for small sample sizes), whereas quantile regression models ($\tau = 0.9$) were compared using $rqAIC_c$ (the AIC_c statistic developed for quantile regression). Akaike weights were computed for models where ΔAIC_c or $\Delta rqAIC_c < 4$. Fivefold, cross-validated AUC (logistic) and R^1 (quantile) provide measures of model fit.

Model class	Candidate models	K	Log-likelihood	AIC_c or $rqAIC_c$	ΔAIC_c or $\Delta rqAIC_c$	w_i	AUC or R^1
	Logistic						
Spatial	Temp + temp^2	3	−9.832	26.708	0.000	0.244	0.855
	Temp + temp^2 + % woody vegetation	4	−8.902	27.621	0.914	0.154	0.811
	% Woody vegetation × temp + temp^2	5	−8.893	30.643	3.940	0.079	0.633
Field covariates included	Temp + temp^2 + % aquatic vegetation	4	−9.306	28.430	1.722	0.103	0.817
	Temp + Temp^2 + % bank slough slump	4	−9.362	28.542	1.835	0.097	0.803
	Temp + temp^2 + residual pool depth	4	−9.567	28.952	2.244	0.079	0.844
	Temp + temp^2 + % cobble	4	−9.658	29.135	2.427	0.072	0.811
	Temp + temp^2 + slope	4	−9.779	29.376	2.668	0.064	0.844
	Temp + temp^2 + Brown Trout (>100 mm) density	4	−9.812	29.441	2.734	0.062	0.794
	Temp + temp^2 + woody vegetation height	4	−9.814	29.446	2.738	0.062	0.750
	Temp + temp^2 + % fines	4	−9.823	29.465	2.757	0.061	0.828
Field only covariates (ΔAIC_c <10)	Residual pool depth	2	−15.495	35.490	8.782		0.594
	Residual pool depth + woody vegetation height	3	−14.413	35.870	9.162		0.622
	Residual pool depth + % cobble	3	−14.730	36.503	9.795		0.550
	Residual pool depth + % bank slough slump	3	−14.760	36.563	9.855		0.678
	Quantile (τ = 0.9)						
Spatial	% Woody vegetation + temp + temp^2	4	−40.650	94.156	6.174	0.040	0.448
	% Woody vegetation × temp + temp^2	5	−40.053	96.306	8.324	0.014	0.461
	Temp + temp^2	3	−44.178	98.174	10.192	0.005	0.371
Field covariates included	Temp + temp^2 + slope	4	−37.562	87.982	0.000	0.873	0.508
	Temp + temp^2 + % cobble	4	−41.586	96.030	8.048	0.016	0.429
	Temp + temp^2 + Brown Trout (>100 mm) density	4	−41.619	96.095	8.113	0.015	0.428
	Temp + temp^2 + % aquatic vegetation	4	−41.705	96.267	8.285	0.014	0.426
	Temp + temp^2 + % fines	4	−42.185	97.226	9.244	0.009	0.416
	Temp + temp^2 + woody vegetation height	4	−42.370	97.596	9.614	0.007	0.412
	Temp + temp^2 + % bank slough slump	4	−42.396	97.649	9.667	0.007	0.412
	Temp + temp^2 + residual pool depth	4	−42.433	97.723	9.741	0.007	0.411
Field only covariates	Slope (%) (only best model shown)	2	−47.849	102.741	14.759		

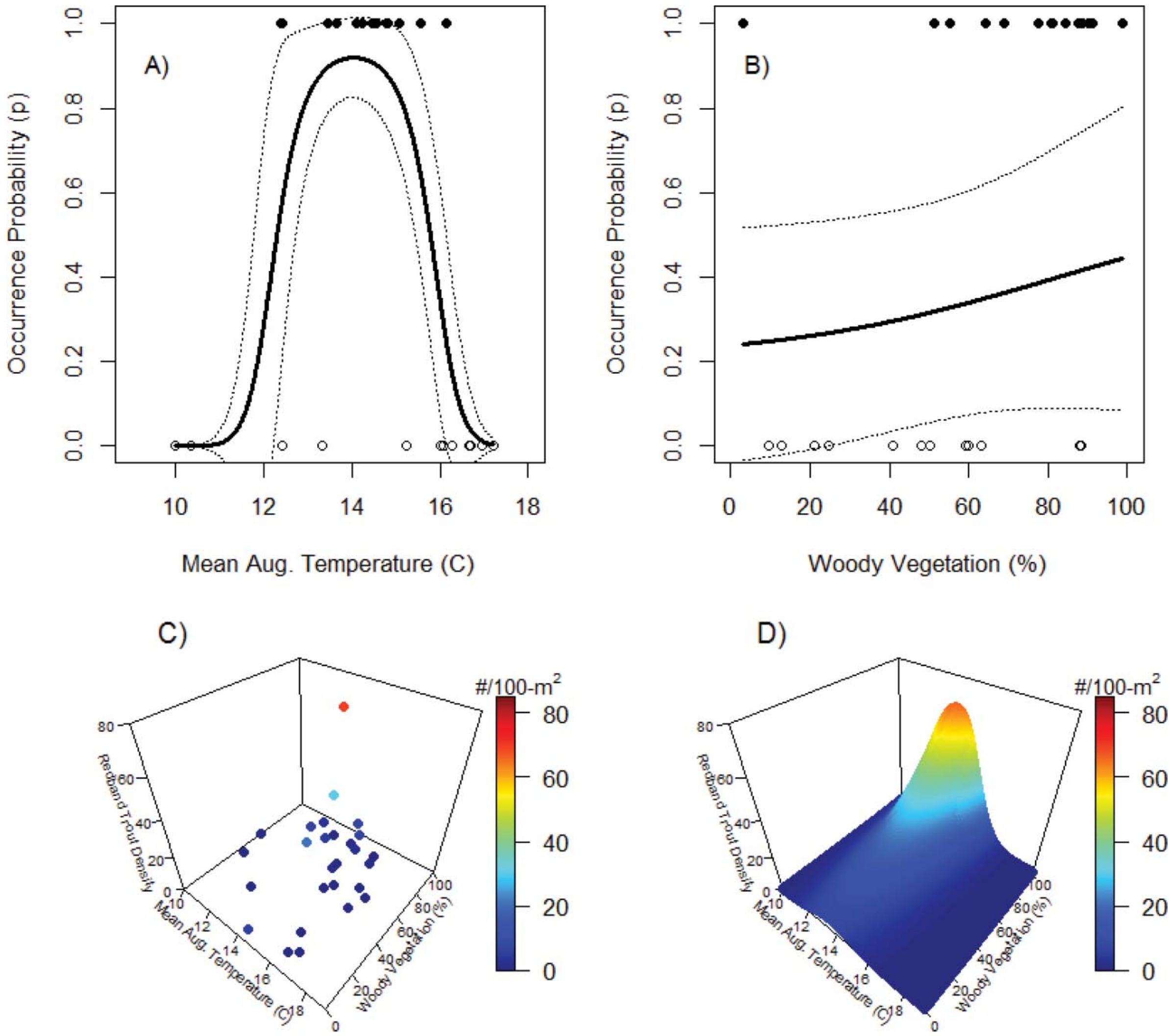

FIGURE 5. Top panels show the predicted Redband Trout occurrence probabilities from a logistic regression model as a function of **(A)** mean August stream temperature and **(B)** percent woody vegetation (classified from NAIP imagery) in Salmon Falls Creek only. The dashed lines represent 90% confidence intervals, and the circles represent observed presences (1; black circles) or absences (0; open circles). The bottom panels represent **(C)** the observed Redband Trout density and **(D)** the predicted densities from a quantile ($\tau = 0.9$) regression model as a function of mean August stream temperature and percent woody vegetation in Salmon Falls Creek only.

Redband Trout density.—Also in Salmon Falls Creek, the candidate quantile regression models with percent woody vegetation and mean August temperature were among the top-ranked models (Table 6). However, the most plausible model was one that contained the two temperature terms and field-measured reach slope. The model explained 50.8% of the variation in the 90th percentile of Redband Trout densities ($R^1_{\tau=0.9} = 0.508$), and no other model was within 6 ΔAIC$_c$ units (Table 6). This model showed the upper quantile ($\tau = 0.9$) of densities to be highest near 13.5°C and higher in steeper streams, although bootstrapped 90% confidence intervals showed high uncertainty at the lowest temperatures and highest slopes (Figure 6). Exploring the next two most plausible models, both with temperature and percent woody vegetation terms, showed them to explain 44.8–46.1% of the variation in the upper quantile of Redband Trout density, and model-averaged parameter estimates (from both models with and without the interaction term) showed densities to be highest at 13.5°C with more woody vegetation (Figure 5D; Table 5). The best model containing only field-measured habitat variables was a single-variable model with stream slope, but it had little support (ΔrqAIC$_c = 14.76$; Table 6).

DISCUSSION

We found that woody riparian vegetation as classified from NAIP imagery, when used in conjunction with spatial predictions of mean August stream temperature from existing models, can be used to characterize Redband Trout habitat in desert streams. With one exception, percent woody vegetation

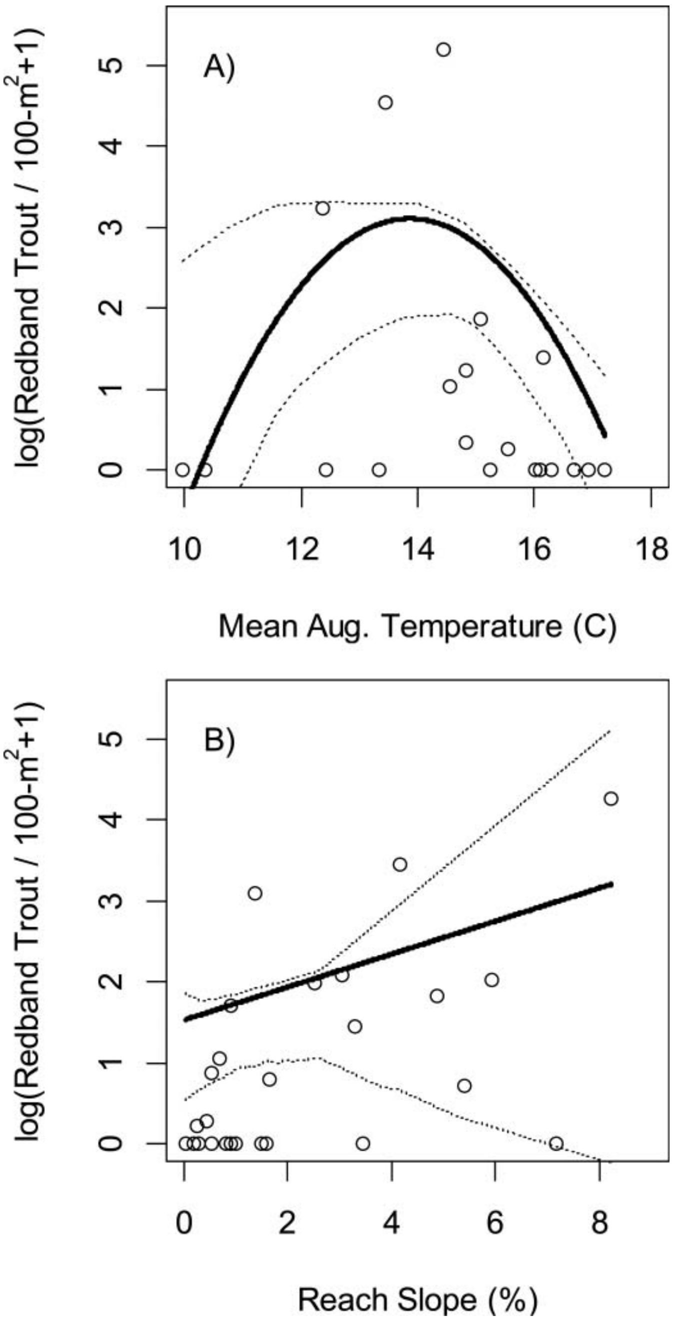

FIGURE 6. Observed and predicted densities of Redband Trout from a quantile ($\tau = 0.9$) regression model as a function of **(A)** stream temperature and **(B)** percent reach slope in Salmon Falls Creek. The dashed lines represent 90% bootstrapped confidence intervals.

as classified from NAIP imagery and modeled stream temperatures together were better descriptors of Redband Trout habitat than temperature and almost all of the instream or riparian habitat variables measured in the field using common habitat assessment protocols. Thus, despite some classification inaccuracy, NAIP imagery and existing spatial predictions of mean August stream temperature together can provide a spatial context to previous field research that has linked Redband Trout density to stream shading and temperature (or surrogates) (Li et al. 1994; Zoellick and Cade 2006). Our study also represents another example of how aerial imagery can be useful in understanding aquatic habitat, species distributions, and stream habitat management needs across large geographic regions.

While models containing woody vegetation together with stream temperature were often the best, or nearly the best, models evaluated, we think that predictions should be used cautiously despite the fact that both woody vegetation and stream temperature are spatial variables that could allow for spatially explicit predictions across northern Nevada and southwestern Idaho (e.g., Dauwalter and Rahel 2008). The models fit for both the Owyhee River and Salmon Falls Creek basins had much less predictive capability than the models fit solely to the Salmon Falls Creek data set. We believe this is largely driven by the fact that most Owyhee River Basin sites were occupied by Redband Trout (84%), which is not surprising since those sites were selected for long-term population monitoring based on previous occurrences of the species. The lack of absences precluded defining well the realized thermal niche of Redband Trout at all sites across both basins. Despite this, the parameter estimate for woody vegetation was precisely estimated and model predictions showed precise predictions of occurrence probability across the range of percent woody vegetation (Figure 3B). In contrast, in Salmon Falls Creek the realized thermal niche was precisely estimated, whereas the effect of woody vegetation was highly uncertain due to both parameter and model uncertainty. Despite the uncertainty, the best occurrence models for Salmon Falls Creek had fivefold, cross-validated AUC values > 0.85, which some consider to be excellent in predictive ability (Hosmer and Lemeshow 2000). Even the quantile regression models explained 45% of the variation in the 90th percentile of Redband Trout densities in Salmon Falls Creek, although prediction intervals were wide at the lowest temperatures (Figure 6A). The fact that our occurrence models had better predictive ability than models predicting Redband Trout densities is not surprising given that it is often easier to predict a species' occurrence than its abundance (Stanfield et al. 2006). Also not surprising is the fact that our models for Salmon Falls Creek had better predictive ability than models fit with data from both basins, as species models often have better predictive ability when fit to data representing smaller spatial domains (Wiley et al. 1997).

We attempted to minimize the influence of spatial autocorrelation by revisiting the sites sampled under a spatially balanced sampling design (GRTS design) and by selecting additional sites on separate Redband Trout populations or separate tributaries within populations. However, we conducted exploratory analyses of correlation in residuals through semivariograms that suggested spatial correlation was evident in our logistic regression models but not our quantile regression models. In fact, the correlation in Redband Trout occurrence was limited from upstream to downstream but not downstream to upstream, and it was prevalent within a distance of 15–50 km (low sample size precluded precise identification of the semivariogram range or the distance at which autocorrelation was absent). The directional autocorrelation suggests that active migration dynamics or downstream juvenile drift may be occurring within populations or "patches" of Redband Trout (Warren et al. 2014). The presence of spatial autocorrelation in species models often leads to a parameter bias near 25%, and accounting for autocorrelation can improve model fit and predictions (Dormann 2007). We explored the use of spatial statistical models for stream networks (Ver Hoef et al. 2006; Peterson et al. 2013) with our data, but we observed mixed results for model selection and fit (comparing spatial to nonspatial models) and thought that our low sample sizes (27 or 52) prohibited the precise estimation of the five extra parameters describing upstream and downstream spatial correlation (exponential models; one nugget, two sill, and two range parameters) in addition to the fixed effects of interest (up to 10 parameters total)(Ver Hoef et al. 2014). If spatial autocorrelation was present in our data, the effects of woody vegetation and temperature were likely underestimated in our models, and it further suggests that there is some underlying factor structuring the occurrence of Redband Trout that was not included in any of our candidate models. The scale and ecological causes of spatial autocorrelation in Redband Trout occurrence (or in other salmonids) should be explored further and will likely require an extensive fish survey database, such as that described by Meyer et al. (2014).

Our NAIP-based land cover data set was 76.0% correct overall, which is slightly less accurate than other widely used land cover data sets derived from the classification of satellite imagery. For example, the National Land Cover Database (NLCD) for 2006 is a land cover classification for the conterminous United States derived from Landsat Thematic Mapper satellite data, with an 85% classification accuracy for the eight main land cover classes (Wickham et al. 2013). Woody vegetation in our analysis was classified as herbaceous riparian or upland vegetation 27% of the time, often because of the strong infrared (greenness) signal of transitional areas between woody vegetation in floodplains and upland vegetation, especially at higher elevations and on north aspect slopes, where vegetation productivity is high outside of the floodplain or riparian zone. This type of misclassification was pronounced at one site in Salmon Falls Creek, where Redband Trout were present but percent woody vegetation classification was estimated to be only 3%. In fact, there was more woody riparian vegetation at that site than was classified, but since our goal was to evaluate the utility of classified NAIP imagery, we retained that apparent outlier in all analyses. Exploratory analysis showed that retaining this site resulted in more uncertainty in the models with woody vegetation as a covariate and less precise parameter estimates, especially for models fit with data from Salmon Falls Creek only. One option we could have pursued was to reclassify that NAIP image to try to improve its classification, which illustrates how classification accuracy can vary image by image and could potentially be controlled to some degree, depending on which individual features or areas in an image required accurate classification.

One advantage of NAIP imagery is its high resolution (1 m) when compared to satellite-derived products. The higher resolution of NAIP imagery allowed for a more accurate classification of thin corridors of woody riparian vegetation (<10 m in width), which would be missed in a classification of 3-m Landsat Thematic Mapper data. While not explicitly part of this study, in Salmon Falls Creek we did compare the predictability of percent woody vegetation as characterized from NAIP imagery (in addition to stream temperature) to percent woody vegetation and percent canopy cover as characterized in the 2006 NLCD (K. A. Fesenmyer, unpublished data). Models with NLCD-based covariates were less plausible than the best model with percent woody vegetation from NAIP imagery ($\Delta AIC_c \geq 1.35$) or a model with temperature covariates only ($\Delta AIC_c \geq 1.62$). In addition, the parameter estimates for the two NLCD-based covariates were estimated to be negative, which contrasts with prior research on the effects of shade from riparian vegetation and topography on Redband Trout density (Zoellick and Cade 2006). The NLCD-based percent canopy is included as a predictor in the NorWeST stream temperature model as a measure of shade, with a parameter estimate that suggests that a 10% increase in percent canopy results in a 0.15°C decrease in mean August stream temperature. Our NAIP-based measure of percent woody vegetation explained additional variance in Redband Trout occurrence and density when compared with modeled temperatures that included percent canopy as a variable. This could be due to the higher resolution of NAIP imagery when compared to the NLCD-based percent canopy derived from 30-m Landsat Thematic Mapper imagery. Or, it could be that we summarized woody vegetation along a higher-resolution hydrography (1:24,000 scale) than that used for the NorWeST model (1:100,000 scale hydrography). Using NAIP-based woody vegetation as a predictor in our models may also have captured its influence on instream habitat beyond shading, such as its effects on stream morphology (e.g., root stabilization of stream banks that reduces sedimentation and creates undercut bank habitat) and terrestrial food subsidies (Wesche et al. 1987; Baxter et al. 2005). Despite its apparent utility in describing riparian vegetation in desert environments, our classification of NAIP imagery in wetter, higher-elevation basins has shown that woody vegetation is less distinguishable from productive emergent grasses and sedges, including hayfields (Fesenmyer, unpublished data).

Despite its utility in characterizing woody streamside vegetation in desert environments, supervised classification of NAIP imagery is time intensive. After a training period, it took about 0.5 h to process a single NAIP image. Across 325 images that equaled 163 h, not including the additional time required to obtain the NAIP imagery and some postprocessing of the classified images. However, the use of aerial imagery can still be more time efficient than field evaluations of riparian vegetation, and it naturally results in spatially continuous data instead of site-specific field data that needs to be extrapolated across an appropriate study area (Booth et al. 2007). In addition, the free availability of NAIP imagery in Google Earth and other GIS software allows users to simply scan and view the imagery to get a quick sense of riparian vegetation conditions and nearby land cover on focal streams without an explicit classification (and the introduction of classification error) and quantification of land cover. Thus, users should evaluate whether NAIP image classification results in a substantial improvement over existing remote-sensing products (or simply viewing the imagery) for their application.

The lack of an overriding influence of instream physical habitat on salmonid distribution and abundance has been shown in other studies. Stream temperature alone has been shown to predict the occurrence of juvenile Bull Trout *Salvelinus confluentus*, as well as more complex models with temperature and other instream habitat variables (Dunham et al. 2003). Likewise, the distribution of multiple salmonid species in the Canadian Rockies has been shown to be largely determined by stream temperature (Paul and Post 2001). Dunham and Vinyard (1997) found that instream habitat in desert streams explained little of the variance in the biomass of Lahontan Cutthroat Trout *O. clarkii henshawi*; biomass was mostly explained by stream-to-stream variation, suggesting that processes (abiotic and biotic) operating at the larger stream scale (>1-km), such as annual streamflow patterns, were influencing populations more than site-specific habitat conditions in 25-m reaches. The inability of physical instream habitat to predict salmonid abundance could be explained by environmental influences at larger scales (Dunham and Vinyard 1997), as well as by variation in the abundance over time due to environmental and demographic factors (Dauwalter et al. 2009; Dochtermann and Peacock 2010). However, it could also be due to the lack of precision with which instream habitat is typically measured and was measured in this study. Some authors have reported that up to 20 transects (spaced every 2–3 mean stream widths) are needed for transect-based sampling to precisely characterize instream habitat (Simonson et al. 1994), and different habitat attributes can be more precisely measured than others (Roper et al. 2002).

Our models reaffirm the importance of both riparian vegetation and temperature to Redband Trout as shown in earlier field and laboratory studies (Zoellick 2004; Zoellick and Cade 2006; Cassinelli and Moffitt 2010). Woody vegetation provides stream shade, can create instream cover and habitat complexity, and can be an important source of terrestrial food subsidies (Wesche et al. 1987; Dauwalter et al. 2014). It also serves as an indicator of perennial streams. Although streamflows in high-desert streams can vary with annual changes in precipitation, woody riparian vegetation requires a consistent water source across multiple years (Busch and Smith 1995; Caplan et al. 2012). Thus, the presence of woody riparian vegetation as observed in NAIP imagery should be useful in determining which streams regularly have enough water to support Redband Trout populations (Zoellick 1999).

The abundance of woody vegetation can also be an indicator of ungulate grazing. Grazing has been shown to reduce riparian vegetation, increase stream temperatures, and, in some cases, result in stream desiccation (Li et al. 1994). It can also increase streambank erosion, resulting in wider and shallower stream channels with shallower pools and increased sedimentation (Li et al. 1994; Bayley and Li 2008). Since riparian vegetation can reflect the broader impacts to streams by ungulate grazing (Clary 1999), NAIP imagery needs to be evaluated as a tool for monitoring the potential impacts of grazing on riparian areas and for identifying streams that are likely candidates for riparian vegetation restoration. Others have also found high-resolution aerial photography to be useful for riparian vegetation monitoring for environmental compliance (Environmental Protection Agency Clean Water Act; Pahl 2010), assessment of stream function (U.S. Bureau of Land Management; Clemmer 2001; Booth et al. 2007), or vegetation recovery due to changes in grazing practices (Booth et al. 2012).

In conclusion, we used object-oriented classification of high-resolution aerial imagery to associate Redband Trout with woody riparian vegetation across a 4-million-ha landscape. Our observation that field-measured habitat was, with one exception, no more predictive of Redband Trout occurrence and density than remotely-sensed measures of woody vegetation suggests that, at a minimum, high-resolution aerial imagery when used in conjunction with existing stream temperature models can be used as a coarse characterization of Redband Trout habitat conditions in desert streams across large geographic areas. This suggests that NAIP and other high-resolution imagery could be a valuable tool for understanding stream habitat conditions for other species with links to woody riparian vegetation in desert environments of the interior western United States.

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REFERENCES

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74: 1175–1178.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201–220.

Bayley, P. B., and H. W. Li. 2008. Stream fish response to grazing exclosures. North American Journal of Fisheries Management 28:135–147.

Benke, R. J. 2002. Trout and salmon of North America. Free Press, New York.

Blaschke, T. 2010. Object based image analysis for remote sensing. Journal of Photogrammetry and Remote Sensing 65:2–16.

Booth, D. T., S. E. Cox, and G. Simonds. 2007. Riparian monitoring using 2-cm GSD aerial photography. Ecological Indicators 7:636–648.

Booth, D. T., S. E. Cox, G. Simonds, and E. D. Sant. 2012. Willow cover as stream-recovery indicator under a conservation grazing plan. Ecological Indicators 18:512–519.

Bozek, M. A., and F. J. Rahel. 1991. Comparison of streamside visual counts to electrofishing estimates of Colorado River Cutthroat Trout fry and adults. North American Journal of Fisheries Management 11:38–42.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information - theoretic approach, 2nd edition. Springer-Verlag, New York.

Burton, T. A., S. J. Smith, and E. R. Cowley. 2011. Riparian area management: multiple indicator monitoring (MIM) of stream channels and streamside vegetation. U.S. Bureau of Land Management, Technical Reference 1737-23, Denver.

Busch, D. E., and S. D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. Ecological Monographs 65:347–370.

Butts, A. E., J. R. Kozfkay, C. Sullivan, and J. C. Dillon. 2011. Fishery management report, Southwest Region 2009. Idaho Department of Fish and Game, Report IDFG 11-108, Boise.

Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. Frontiers in Ecology and Environment 1:412–420.

Cade, B. S., B. R. Noon, and C. H. Flather. 2005. Quantile regression reveals hidden bias and uncertainty in habitat models. Ecology 86:786–800.

Caplan, T. R., K. Cothern, and Landers. 2012. Cuttings in relation to alluvial soil texture and water availability. Restoration Ecology 21: 627–638.

Carpenter, K. D., C. R. Czuba, C. S. Magirl, M. D. Marineau, S. Sobieszczyk, J. A. Czuba, and M. K. Keith. 2012. Geomorphic setting, aquatic habitat, and water-quality conditions of the Molalla River, Oregon, 2009-10. U.S. Geological Survey, Scientific Investigations Report 2012-5017, Reston, Virginia.

Cassinelli, J. D., and C. M. Moffitt. 2010. Comparison of growth rates and stress in resident Redband Trout held in laboratory simulations of montane and desert summer temperature cycles. Transactions of the American Fisheries Society 139:339–352.

Clary, W. P. 1999. Stream channel and vegetation responses to late spring cattle grazing. Journal of Rangeland Management 52:218–227.

Clemmer, P. 2001. Riparian area management: the use of aerial photography to manage riparian-wetland areas. U.S. Bureau of Land Management, Technical Reference 1737-10, Denver.

Cleve, C., M. Kelly, F. R. Kearns, and M. Moritz. 2008. Classification of the wildland-urban interface: a comparison of pixel- and object-based classifications using high-resolution aerial imagery. Computers, Environment and Urban Systems 32:317–326.

Cross, B. K., M. A. Bozek, and M. G. Mitro. 2013. Influences of riparian vegetation on trout stream temperatures in central Wisconsin. North American Journal of Fisheries Management 33:682–692.

Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. American Midland Naturalist 67:477–504.

Dauwalter, D. C., and F. J. Rahel. 2008. Distribution modeling to guide stream fish conservation: an example using the mountain sucker in the Black Hills National Forest, USA. Aquatic Conservation: Marine and Freshwater Ecosystems 18:1263–1276.

Dauwalter, D. C., F. J. Rahel, and K. G. Gerow. 2009. Temporal variation in trout populations: implications for monitoring and trend detection. Transactions of the American Fisheries Society 138:38–51.

Dauwalter, D. C., S. J. Wenger, and P. Gardner. 2014. The role of habitat complexity in habitat use and selection by stream fishes in a Snake River basin tributary. Transactions of the American Fisheries Society 143:1177–1187.

Dauwalter, D. C., S. J. Wenger, K. R. Gelwicks, and K. A. Fesenmyer. 2011. Land use associations with declining native fishes in the upper Colorado River basin. Transactions of the American Fisheries Society 140:646–658.

Dochtermann, N. A., and M. M. Peacock. 2010. Differences in population size variability among populations and species of the family Salmonidae. Journal of Animal Ecology 79:888–896.

Dormann, C. F. 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Global Ecology and Biogeography 16:129–138.

Dunham, J., B. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of Bull Trout within streams at the southern margin of its range. North American Journal of Fisheries Management 23:894–904.

Dunham, J. B., and G. L. Vinyard. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. Transactions of the American Fisheries Society 126:323–329.

Harrelson, C. C., C. L. Rawlins, and J. P. Potyondy. 1994. Stream channel reference sites: an illustrated guide to field technique. U.S. Forest Service General Technical Report RM-245.

Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman, and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18(6):3–12.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression, 2nd edition. Wiley, New York.

Hughes, R. M., L. Wang, and P. W. Seelbach, editors. 2006. Landscape influences on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Isaak, D. J., C. H. Luce, B. E. Rieman, D. E. Nagel, E. E. Peterson, D. L. Horan, S. Parkes, and G. L. Chandler. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. Ecological Applications 20:1350–1371.

Isaak, D. J., M. K. Young, D. E. Nagel, D. L. Horan, and M. C. Groce. 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Global Change Biology 21:2540–2553.

Johnson, D. H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763–772.

Koenker, R. 2013. quantreg: quantile regression, R package version 5.05. Available: http://www.r-project.org. (October 2015).

Kozfkay, J. R., A. E. Butts, and J. C. Dillon. 2011. Fishery management report, Southwest Region 2010. Idaho Department of Fish and Game, Report IDFG 11-110, Boise.

Leglieter, C. J. 2013. Mapping river depth from publically available aerial images. River Research and Applications 29:760–780.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, J. L. Li, and J. C. Buckhouse. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society 123:627–640.

Lillesand, T. M., and R. W. Kiefer. 2000. Remote sensing and image interpretation, 4th edition. Wiley, New York.

Lukacs, P. M., K. P. Burnham, and D. R. Anderson. 2010. Model selection bias and Freedman's paradox. Annals of the Institute of Statistical Mathematics 62:117–125.

Meyer, K. A., J. A. Lamansky Jr., and D. J. Schill. 2010. Biotic and abiotic factors related to Redband Trout occurrence and abundance in desert and montane streams. Western North American Naturalist 70:77–91.

Meyer, K. A., D. J. Schill, E. R. J. Mamer, C. C. Kozfkay, and M. R. Campbell. 2014. Status of Redband Trout in the upper Snake River basin of Idaho. North American Journal of Fisheries Management 34:507–523.

Muhlfeld, C. C., S. E. Albeke, S. L. Gunckel, B. J. Writer, B. B. Shepard, and B. E. May. 2015. Status and conservation of interior Redband Trout in the western United States. North American Journal of Fisheries Management 35:31–53.

Ogle, D. H. 2013. FSA: fisheries stock analysis, R package version 0.4.30. Available: https://fishr.wordpress.com/fsa. (October 2015).

Pahl, R. 2010. Dixie and Hanks creeks temperature TMDLs. Nevada Department of Environmental Protection, Carson City.

Paul, A. J., and J. R. Post. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. Transactions of the American Fisheries Society 130:417–430.

Peterson, E. E., J. M. Ver Hoef, D. J. Isaak, J. A. Falke, M.-J. Fortin, C. E. Jordan, K. McNyset, P. Monestiez, A. S. Ruesch, A. Sengupta, N. Som, E. A. Steel, D. M. Theobald, C. E. Torgersen, and S. J. Wenger. 2013. Modelling dendritic ecological networks in space: an integrated network perspective. Ecology Letters 16:707–719.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.

R Core Team. 2015. R: a language and environment for statistical computing, version 3.0.2. R Foundation for Statistical Computing, Vienna.

Roper, B. B., J. L. Kershner, E. Archer, R. Henderson, and N. Bouwes. 2002. An evaluation of physical stream habitat attributes used to monitor streams. Journal of the American Water Resources Association 38:1637–1646.

Rose, R. A., D. Byler, J. R. Eastman, E. Fleishman, G. Geller, S. Goetz, L. Guild, H. Hamilton, M. Hansen, R. Headley, J. Hewson, N. Horning, B. A. Kaplin, N. Laporte, A. Leidner, P. Leimgruber, J. Morisette, J. Musinsky, L. Pintea, A. Prados, V. C. Radeloff, M. Rowen, S. Saatchi, S. Schill, K. Tabor, W. Turner, A. Vodacek, J. Vogelmann, M. Wegmann, D. Wilkie, and C. Wilson. 2014. Ten ways remote sensing can contribute to conservation. Conservation Biology 29:350–359.

Schill, D. J., G. W. LaBar, E. R. J. Mamer, and K. A. Meyer. 2010. Sex ratio, fecundity, and models predicting length at sexual maturity of Redband Trout in Idaho desert streams. North American Journal of Fisheries Management 30:1352–1363.

Shealer, D. A., and M. J. Alexander. 2013. Use of aerial imagery to assess habitat suitability and predict site occupancy for a declining wetland-dependent bird. Wetlands Ecology and Management 21:289–296.

Simonson, T. D., J. Lyons, and P. D. Kanehl. 1994. Quantifying fish habitat in streams: transect spacing, sample size, and a proposed framework. North American Journal of Fisheries Management 14:607–615.

Stanfield, L. W., S. F. Gibson, and J. A. Borwick. 2006. Using a landscape approach to identify the distribution and density patterns of salmonids in Lake Ontario tributaries. Pages 601–621 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Landscape influences on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Tamminga, A., C. Hugenholtz, B. Eaton, and M. Lapointe. 2015. Hyperspatial remote sensing of channel reach morphology and hydraulic fish habitat using an unmanned aerial vehicle (UAV): a first assessment in the context of river research and management. River Research and Applications 31:379–391.

Valta-Hulkkonen, K., A. Kanninen, R. Ilvonen, and J. Leka. 2005. Assessment of erial photography as a method for monitoring aquatic vegetation in lakes of varying trophic status. Boreal Environment Research 10:57–66.

Vatland, S. J., R. E. Gresswell, and G. C. Poole. 2015. Quantifying streamthermal regimes atmultiple scales: combining thermal infrared imagery and stationary stream temperature data in a novelmodeling framework. Water Resources Research 51:31–46.

Ver Hoef, J. M., E. E. Peterson, D. Clifford, and R. Shah. 2014. SSN: an R package for spatial statistical modeling on stream networks. Journal of Statistical Software 56:1–45.

Ver Hoef, J. M., E. Peterson, and D. Theobald. 2006. Spatial statistical models that use flow and stream distance. Environmental and Ecological Statistics 13:449–464.

Warren, D. R., J. B. Dunham, and D. Hockman-Wert. 2014. Geographic variability in elevation and topographic constraints on the distribution of native and nonnative trout in the Great Basin. Transactions of the American Fisheries Society 143:205–218.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences of the USA 108:14175–14180.

Wesche, T. A., C. M. Goertler, and C. B. Frye. 1987. Contribution of riparian vegetation to trout cover in small streams. North American Journal of Fisheries Management 7:151–153.

Wickham, J. D., S. V. Stehman, L. Gass, J. Dewitz, J. A. Fry, and T. G. Wade. 2013. Accuracy assessment of NLCD 2006 land cover and impervious surface. Remote Sensing of Environment 130:294–304.

Wiley, M. J., S. L. Kohler, and P. W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. Freshwater Biology 37:133–148.

Wirth, L., A. E. Rosenberger, A. Prakash, R. Gens, F. J. Margraf, and T. Hamazaki. 2012. A remote-sensing, GIS-based approach to identify, characterize, and model spawning habitat for fall-run chum salmon in a sub-arctic, glacially fed river. Transactions of the American Fisheries Society 141:1349–1363.

Wolock, D. M. 2003. Base-flow index grid for the conterminous United States. U.S. Geological Survey, Reston, Virginia.

Wondzell, S. M., M. A. Hemstrom, and P. A. Bisson. 2007. Simulating riparian vegetation and aquatic habitat dynamics in response to natural and anthropogenic disturbance regimes in the upper Grande Ronde River, Oregon, USA. Landscape and Urban Planning 80:249–267.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82–90.

Zoellick, B. W. 1999. Stream temperatures and the elevational distribution of Redband Trout in southwestern Idaho. Great Basin Naturalist 59:136–143.

Zoellick, B. W. 2004. Density and biomass of Redband Trout relative to stream shading and temperature in southwestern Idaho. Western North American Naturalist 64:18–26.

Zoellick, B. W., D. B. Allen, and B. J. Flatter. 2005. A long-term comparison of Redband Trout distribution, density, and size structure in southwestern Idaho. North American Journal of Fisheries Management 25:1179–1190.

Zoellick, B. W., and B. S. Cade. 2006. Evaluating Redband Trout habitat in sagebrush desert basins in southwestern Idaho. North American Journal of Fisheries Management 26:268–281.