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Climate change and vulnerability of bull trout (*Salvelinus confluentus*) in a fire-prone landscape

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Abstract: Linked atmospheric and wildfire changes will complicate future management of native coldwater fishes in fire-prone landscapes, and new approaches to management that incorporate uncertainty are needed to address this challenge. We used a Bayesian network (BN) approach to evaluate population vulnerability of bull trout (*Salvelinus confluentus*) in the Wenatchee River basin, Washington, USA, under current and future climate and fire scenarios. The BN was based on modeled estimates of wildfire, water temperature, and physical habitat prior to, and following, simulated fires throughout the basin. We found that bull trout population vulnerability depended on the extent to which climate effects can be at least partially offset by managing factors such as habitat connectivity and fire size. Moreover, our analysis showed that local management can significantly reduce the vulnerability of bull trout to climate change given appropriate management actions. Tools such as our BN that explicitly integrate the linked nature of climate and wildfire, and incorporate uncertainty in both input data and vulnerability estimates, will be vital in effective future management to conserve native coldwater fishes.

Résumé : Les interactions entre les changements atmosphériques et les feux de forêt compliqueront la gestion future des poissons d'eau froide indigènes dans les paysages à risque élevé d'incendie, et de nouvelles approches de gestion qui intègrent l'incertitude sont nécessaires pour relever le défi que cela posera. Nous avons utilisé une approche de réseaux bayésiens (RB) pour évaluer la vulnérabilité de la population d'ombles à tête plate (*Salvelinus confluentus*) dans le bassin versant de la rivière Wenatchee (État de Washington, États-Unis), étant donné différents scénarios climatiques et d'incendie présents et futurs. Le RB reposait sur des estimations modélisées des feux de forêt, de la température de l'eau et de l'habitat physique avant et après des incendies simulés à la grandeur du bassin versant. Nous avons constaté que la vulnérabilité de la population d'ombles à tête plate dépendait de la mesure dans laquelle les effets du climat peuvent être au moins partiellement compensés par la gestion de facteurs comme la connectivité de l'habitat et la taille des feux. En outre, notre analyse montre qu'une gestion locale comprenant des mesures de gestion adéquates peut réduire de manière significative la vulnérabilité de l'omble à tête plate aux changements climatiques. Des outils comme l'approche basée sur les RB qui intègre explicitement le lien entre le climat et les feux de forêt et qui incorpore l'incertitude des données entrantes et des estimations de la vulnérabilité seront des éléments clés d'une gestion efficace visant la conservation des poissons d'eau froide indigènes. [Traduit par la Rédaction]

Introduction

In the Pacific Northwest United States, air temperature has increased by >1 °C since 1920. By 2080, temperature will likely increase another 2 °C, snowpack will continue to decline, and drought frequency will increase (Climate Impacts Group 2009). Likewise, the prospect of a warmer–drier climate in this region portends increased frequency, severity, and size of wildfires (McKenzie et al. 2004; Westerling et al. 2006; Liu et al. 2013). These linked atmospheric and wildfire changes will influence terrestrial and freshwater ecosystems. In streams, climate changes are decreasing flows (Stewart et al. 2005; Luce and Holden 2009; Arismendi et al. 2013) and in some cases increasing stream temperatures (Arismendi et al. 2012; Isaak et al. 2012). Large and severe wildfires also characteristically lead to increased stream temperatures (Dunham et al. 2007; Isaak et al. 2010; Mahlum et al. 2011), which may extirpate coldwater fish populations, particularly

where habitats are fragmented or degraded by other factors (e.g., land use; Brown et al. 2001; Dunham et al. 2003b; Rieman et al. 2003). Given the strong relations between wildfires and climatic warming, and their joint impacts on freshwaters, it is critical to consider both when managing vulnerable fish species, including salmonids (salmon and trout; Bisson et al. 2003; Rieman and Isaak 2010).

Among salmonids in the Pacific Northwest, the bull trout (*Salvelinus confluentus*) has some of the coldest water requirements (Selong et al. 2001; Dunham et al. 2003a), with the possible exception of the closely related Dolly Varden (*Salvelinus malma*; Dunham et al. 2008), and is dependent on the presence of large, interconnected habitat patches year-round (Dunham and Rieman 1999). At present, the bull trout is listed as a threatened species under the US Endangered Species Act (ESA; US Fish and Wildlife Service 2008). Furthermore, knowledge of climate change and wildfire threats to bull trout is incomplete, and there is great uncertainty

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surrounding management of future threats (Rieman and Isaak 2010; Peterson et al. 2013; Wenger et al. 2013). Some uncertainty stems from a lack of tools for incorporating knowledge about threats to concrete applications at local scales where management decisions are made. Our objective here was to address this need for bull trout in fire-prone watersheds and develop an approach that could be adapted to other species with similar habitat requirements or to multiple species with different biological requirements within a common domain (e.g., Rieman et al. 2000).

To better understand the effects of wildfires on coldwater fish, plausible scenarios must be considered that incorporate terrestrial (e.g., vegetation treatments) and aquatic (e.g., fish passage) ecosystem management actions (Dunham et al. 2003b) alongside natural physical and biological processes that influence aquatic (e.g., stream hydrology and heating; Miller et al. 2003; Wondzell and King 2003) and terrestrial ecosystems (e.g., successional patch dynamics and resilient patch size distributions; Moritz et al. 2011; Perry et al. 2011) in the context of climatic warming (Bisson et al. 2003; Rieman et al. 2010). One useful approach to evaluating these scenarios in the face of incomplete information involves the application of Bayesian network (BN) analysis (Pearl 2000; Jensen 2001). Properties of BN analysis that are relevant to considering wildfire and climate effects on fish include the ability to (i) integrate both qualitative and quantitative information from disparate sources, (ii) predict relative differences in expected outcomes from multiple scenarios, (iii) incorporate and track uncertainty, and (iv) modify the network to account for new knowledge and data. BNs have been successfully used as a tool for biological conservation in numerous cases (Marcot et al. 2006, etc.), and salmonid conservation in particular (Rieman et al. 2001; Borsuk et al. 2006; Peterson et al. 2008; Roberts et al. 2013).

We used BN analysis here to evaluate the threat to bull trout posed by wildfire influences on habitat suitability and fragmentation (sensu Dunham et al. 2003b). Initial conditions in our study watershed were determined by modeled patterns of stream temperature, which were then used to delineate continuously suitable bull trout habitat patches (Dunham et al. 2002; Isaak et al. 2010). Impacts of simulated wildfires, modeled stream temperatures, and the local climate on bull trout habitat variables (stream size, temperature, and winter stream discharge; Wenger et al. 2011a) were jointly considered using a BN (see also Peterson et al. 2013) to predict population vulnerability across a set of scenarios. Modeled scenarios included a range of climatic futures and a spectrum of actions to manage surface and canopy fuels and improve fish passage.

Materials and methods

Study area

Our study area was the Wenatchee River basin in Washington, USA (Table 1; Fig. 1). The Wenatchee River and its tributaries originate east of the Cascade Mountain crest and drain approximately 3451 km² of the North Cascades ecoregion (Wiken et al. 2011). Contemporary climate in the basin is continental, characterized by warm, dry summers, variably cold winters and snow accumulations, and peak stream flows associated with snowmelt in May–June (Climate Impacts Group 2009). Vegetation is characterized by dry grasslands and shrublands below the lower treeline, dry and mesic mixed conifer forests in low and mid-montane settings — composed mainly of ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), and Douglas-fir (*Pseudotsuga* sp.) — and subalpine forests in upper montane environments. Fire suppression, timber harvest, overgrazing (Bisson et al. 2003; Hessburg and Agee 2003; Hessburg et al. 2005, 2007), and climate change during the last century have altered the fire regime in the region (McKenzie et al. 2004; Littell et al. 2009, 2010; Westerling et al. 2006). These influences have led to large accumulations of dead wood, development of dense forests, and ongoing

Table 1. Summary statistics and count of bull trout habitat patches within seven subwatersheds in the Wenatchee River basin, Washington, USA.

Subwatershed	Watershed area (ha)	Stream length (km)	No. of patches
Chiwawa River	48 608	352.6	1
Chiwaukum Creek	21 956	154.0	1
Icicle Creek	55 439	373.6	2
Little Wenatchee River	40 671	249.9	1
Nason Creek	27 991	188.5	1
Peshastin Creek	34 845	262.7	4
White River	26 225	194.0	1

insect outbreaks and disease epidemics that have combined with the cumulative effects of drought to exacerbate the severity and magnitude of wildfires (Hessburg et al. 1999, 2000; McKenzie et al. 2004; Littell et al. 2009, 2010).

Historically, wildfires were common to eastern Cascade Mountain forests, with mean fire-free intervals of less than 10 years (e.g., Everett et al. 2000). Following the advent of effective wildfire suppression (1934–1935) and related forest management activities in the early 20th century, this interval increased dramatically (e.g., 15–60 years in forests studied by Everett et al. 2000). However, wildfire activity continues, with recent fires in the Icicle Creek drainage in 1994, 2001, and 2004 (McElroy et al. 2005). The median total area burned in the Okanogan–Wenatchee National Forest (OWNF) during the period 1984–2010 was 1097 ha, but varied by an order of magnitude among years ($n = 196$; range 53 – 50 025 ha; Monitoring Trends in Burn Severity (MTBS) database; <http://www.mtbs.gov>; Fig. 2).

Over the past several decades, federal land management in the Wenatchee River basin has employed surface and canopy fuels treatments (Townsend et al. 2004) to reduce the risk of wildfires (e.g., precommercial, low, and free-thinning), and prescribed underburns to reduce seedling and sapling recruitment as well as reduce fuel ladders and surface fuels (Graham et al. 1999, 2004). Although the treated area has increased threefold during the period 1990–2003, treated area outside of wilderness is small (~1% of forest area) relative to historical annual burned area (~2%–5%, Barrett et al. 1997). While these efforts have reduced wildfire threat locally, the likelihood of large future wildfires is great (Gedalof and Smith 2001; Hessl et al. 2004; McKenzie et al. 2004).

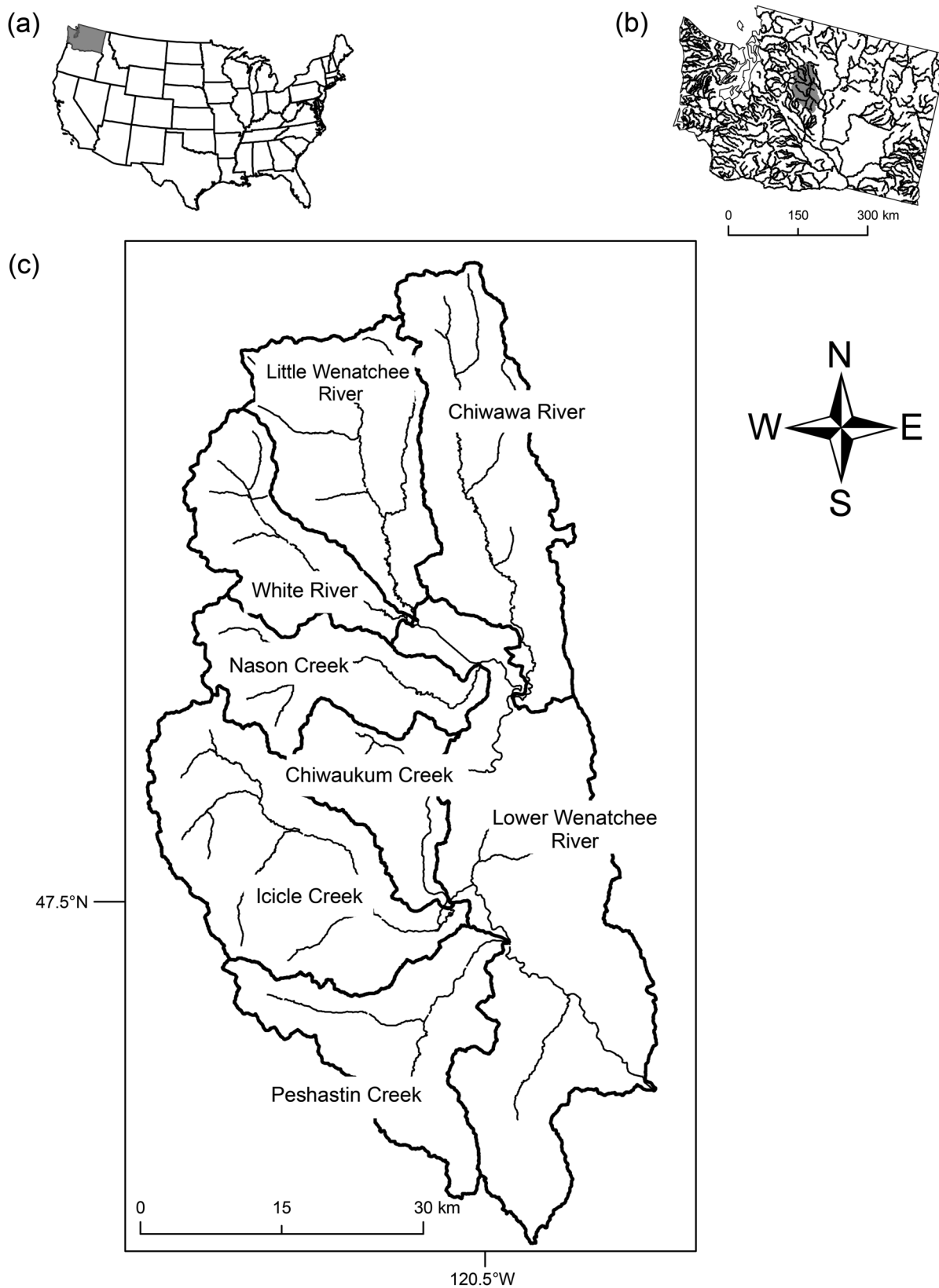
Model of bull trout vulnerability

We employed a BN modeling approach to assess the vulnerability of bull trout to changes in local habitat suitability, wildfires, and fragmentation (e.g., Dunham et al. 2003b). Interactions among these factors were driven by climate, stream hydrography, landform, and spatial patterns of thermal variation and were modeled to evaluate their collective influence on bull trout population vulnerability. To implement the BN, we used Netica version 4.6 software (Norsys Software Corp., Vancouver, British Columbia), which allowed us to estimate error propagation and uncertainty of vulnerability predictions. We applied the resulting model to evaluate bull trout vulnerability to wildfires in the Wenatchee River basin under six scenarios that considered three climatic futures and two climate-adaptation management strategies.

Model setting

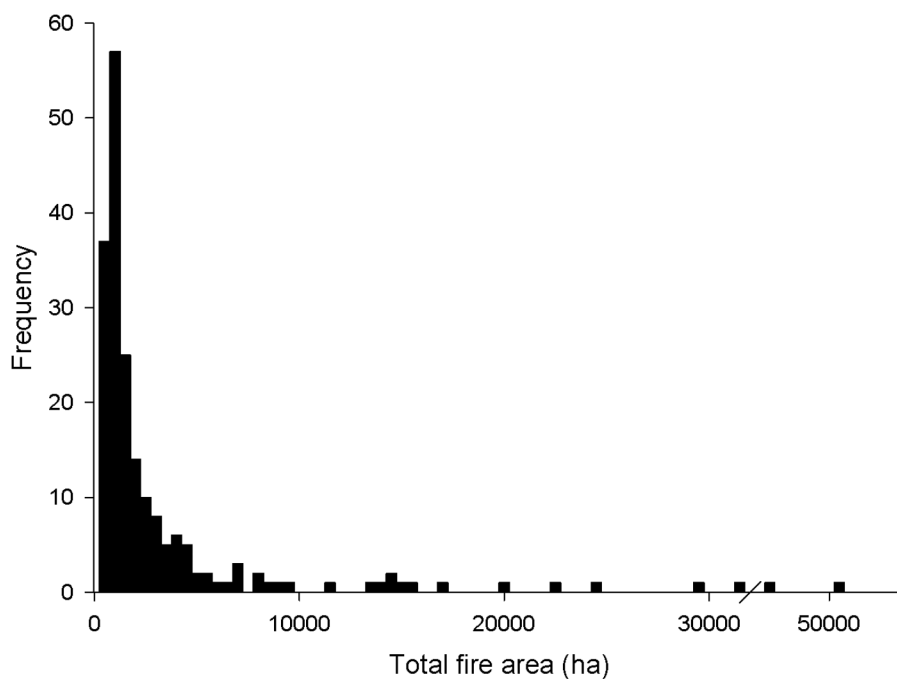
The BN modeling environment consisted of four combined elements: the stream network, patterns of temperature within the network, corresponding patterns of suitable habitat based on physical characteristics, and probable patterns of fire severity (Fig. 3). We describe each in turn below.

Fig. 1. (a) Study area in the Wenatchee River basin located in (b) central Washington, USA. The locations of major tributaries in eight sub-basins are shown in panel (c).



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Fig. 2. Histogram of wildfire sizes (ha) for the Wenatchee–Okanogan National Forest. Data represent fires occurring during the period 1984–2012 (<http://www.mtbs.gov>).



Stream network

We used the functional linkage of water basins and streams (FLoWS) version 9.3 toolbox (Theobald et al. 2006) for ArcGIS 9.3.1 (ESRI 2009) to create a digital representation of the hydrologic network, based on the 1 : 100 000 scale hydrography layer obtained from National Hydrography Dataset (<http://nhd.usgs.gov>), and clipped in a geographical information system (GIS) to the domain of the Wenatchee River basin. From these, we generated topological relations among all stream reaches in the GIS, where a reach was defined as the stream length between confluences. We used FLoWS to identify the unique land surface area draining into each reach (reach contributing area; RCA) using the digital hydrography layer and a 10 m digital elevation model (DEM; National Elevation Dataset; <http://ned.usgs.gov>). The one-to-one relation between reaches and RCAs allowed us to link relevant portions of the terrestrial landscape to stream reaches, and to calculate scaled drainage areas. Using the topological relationships generated by FLoWS and customized scripts implemented in C++, we measured in-stream distances (km) among reaches, along with other metrics (see Vulnerability analysis section).

We evaluated bull trout habitat relations at patch and reach scales (Fig. 4; see Habitat patch delineation section); individual reaches (mean (\pm standard deviation, SD) length = 1.9 ± 1.3 km) and their associated RCAs were nested within patches. Variables used in BN analyses were summarized to reaches or systematically estimated every 200 or 1000 m, depending on the spatial resolution of the available data. We report model results at reach and patch scales.

Habitat patch delineation

For coldwater specialists like bull trout, the spatial distribution of suitable habitats is typically fragmented into discrete patches within the stream network (Rieman and McIntyre 1995; Dunham and Rieman 1999). Using results of a stream temperature model (see Stream temperature section), we defined cold-water patches suitable to bull trout as continuous stream reaches with maximum summer temperatures ≤ 17 °C (Fig. 4). This threshold is consistent with observations of increasing bull trout presence (Dunham et al. 2003a) and is below the maximum temperature for

indefinite growth and survival given sufficient food (Selong et al. 2001).

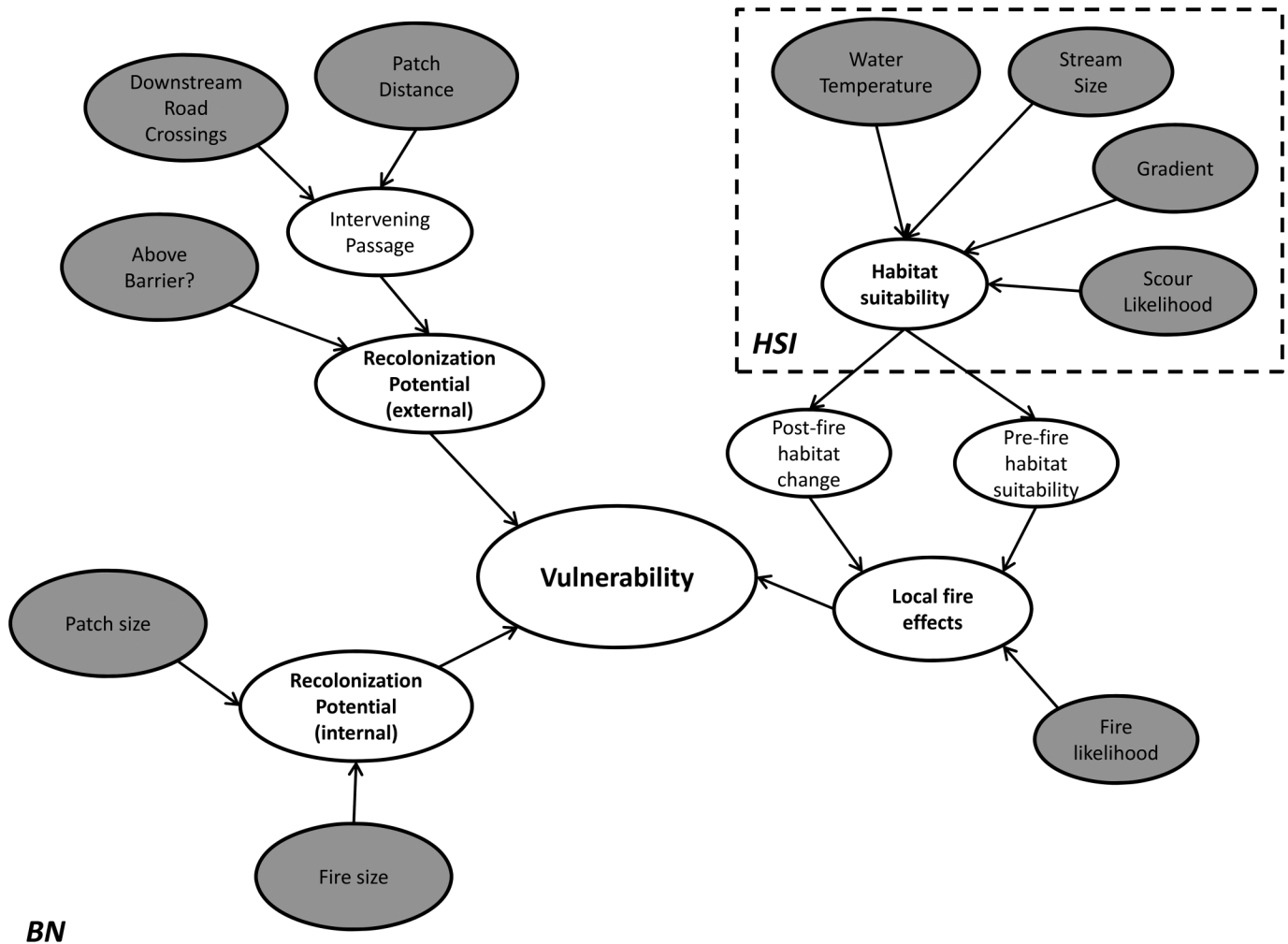
Wildfire likelihood and severity

Spatially explicit estimates of wildfire burn severity were generated using a modified version of FlamMap version 5 (Finney 2002, 2003, 2005, 2006), a fire growth model that simulates wildfire behavior (<http://www.firelab.org/project/flammap>). FlamMap uses spatial information on topography and fuels to calculate fire behavior characteristics for a single set of environmental conditions (i.e., constant wind, weather, and fuel moisture). We relaxed the constant weather assumptions in our simulations and instead predicted flame lengths (FL) and fireline intensities (FLI) using five equi-probable wind directions (210°, 240°, 270°, 300°, and 330° true) that are typical in the basin under average fire season burn conditions. We used WindNinja (Forthofer 2007) to simulate wind flow routing assuming these five wind directions, and used the resulting wind grids to initialize FlamMap. Wind speed was set to $24 \text{ km}\cdot\text{h}^{-1}$ at 6.1 m of vertical height. A total of 100 000 wildfire ignitions were simulated, and the resulting maps were used to estimate probable FL and FLI across all wildfires. The most probable FL and FLI classes across all simulated fires were translated into probable wildfire severity classes (low, moderate, and high), and these values were mapped at 30 m^2 resolution. Surface fuels used in the FlamMap simulations were mapped by OWNF personnel and are available upon request. Canopy fuels used to initialize the FlamMap simulations were derived from LANDFIRE data layers (<http://www.landfire.gov>). Vegetation types (i.e., forest species composition and structure characteristics) were based on geospatial data developed by the Landscape Ecology Management and Mapping (LEMMA) group (<http://www.fsl.orst.edu/lemma/splash.php>).

Stream temperature

We used a spatially and temporally continuous stream water temperature model to predict mean annual maximum temperature (TMAX; °C), pre- and post-wildfire, every 1000 m along the stream network. Continuous temperature estimates were generated over 2001–2010 using in situ stream temperature data and

Fig. 3. Conceptual diagram depicting environmental processes hypothesized to affect bull trout population persistence in fire-prone landscapes. Shaded ovals represent input variables in the belief network (BN). Variables within the dashed box represent those contributing to a bull trout habitat suitability index (HSI), whereas those outside the box represented factors contributing to bull trout population vulnerability. See Table 2 for definitions of nodes and states within nodes.



remotely sensed land surface temperature (LST) from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS; NASA 2013). The temporal grain or resolution of our analysis (estimated maximum temperatures) was 8 days (as opposed to the conventional 7-day week), based on the resolution of MODIS observations. In the model, the estimated maximum temperature, based on an 8-day window of observation, was defined as TMAX. In streams such as the ones that we studied (relatively cool with lower diurnal fluctuations), daily and weekly maximum temperatures are strongly correlated (Dunham et al. 2005). Fifty sets of stream temperature data were acquired from the OWNF and the National Oceanic and Atmospheric Administration (NOAA). We used regression analysis to relate LST to water temperature, following the methods of Falke et al. (2013) and K.M. McNyset (unpublished data), and calculated annual and decadal temperature summaries.

Severity data from seven OWNF wildfires occurring from 2000 to 2008 were acquired from the MTBS database and used to quantify the observable changes in LST postfire for each fire severity class (unburned, low, moderate, and high). An annual model of the expected change in postfire LST for each fire severity class was developed using a multivariate adaptive regression splines (MARS) hinge function in the *mda* package in R software (R Development Core Team 2010). Postfire LST estimates were used to

generate stream temperature estimates every 1000 m throughout the stream network (K.M. McNyset, unpublished data).

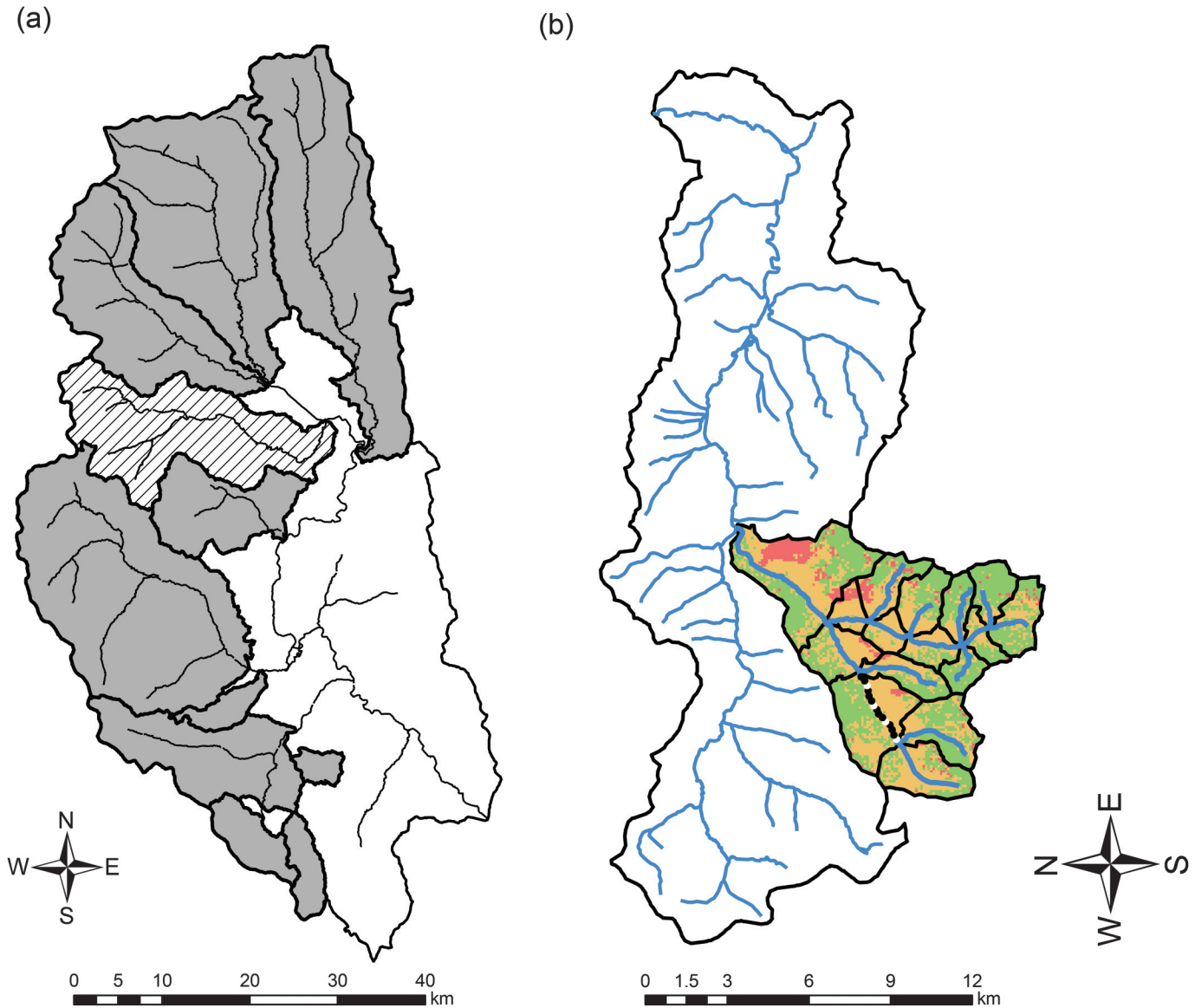
Vulnerability of bull trout

We modeled bull trout vulnerability as a function of habitat suitability, wildfire effects, habitat connectivity, and patch size (e.g., Dunham et al. 2003a; Peterson et al. 2013). Combinations of these factors varied in the BN model (Fig. 3), which we describe below.

Habitat suitability

We developed a habitat suitability index (HSI) to characterize the quality of spawning and rearing habitats potentially used by bull trout. Variables used in the HSI (i) were reported in the peer-reviewed literature and included uncertainty estimates for each parameter (e.g., SE); (ii) are basic components of habitat that are important controls on bull trout distribution across the species' range (e.g., to facilitate transfer to other basins); (iii) can be estimated and mapped continuously across broad regions; and (iv) were based on observations from studied river systems similar to the Wenatchee River basin. Using these four criteria, we identified stream temperature, size, gradient, and scour likelihood (detailed below) as four predictors upon which to base the HSI.

Fig. 4. Coldwater patches (*a*; gray shading) and an illustration of scales of analysis used in this study for one patch (*b*; hatched polygon). Reaches were defined as the length of stream from one confluence to the next (blue lines), and polygons are reach contributing areas (RCA's). Points are where estimates of covariates were made every 200 m (filled) and 1 km (open). Fire severity (red, high; yellow, moderate; green, low) is also shown for an example drainage. For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2014-0098>.



Values of each predictor were calculated every 200 m throughout the stream network ($n = 12\,409$) and used as input data to the BN.

Bull trout occurrence probability (ψ) was predicted as a function of the four predictors that were primary nodes in our BN. The four probabilities, initially predicted as four continuous variables, were each reclassified into categorical variables exhibiting low (0–0.32), moderate (0.33–0.66), or high (>0.66) values (Table 2). Conditional probabilities defining relations among nodes were estimated from empirically derived logistic functions that incorporated errors associated with intercept (β_0) and slope (β_1) estimates of covariate (x), and whose general formula was

$$(1) \quad P(\psi|x, \beta_0, \beta_1) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x)}}$$

Equations and conditional probability tables (CPTs) can be found in the online Supplementary data¹. We verified that parameter estimates and errors were normally distributed, $X \sim N(\mu, \sigma^2)$, for all occurrence–habitat relations in the HSI. Equations for each of the four HSI variables were taken from previously published logistic regressions (stream size, winter stream flow, and stream gradient: Wenger et al. 2011a; stream temperature: Dunham et al. 2003a).

Thus, predicted ψ probabilities were derived for every 200 m along the stream network for each predictor, continuous values of each were reclassified, and the four component conditions were used to assign a composite HSI categorical value of low, moderate, or high. Composite values reflected weighted combinations of the four predictors. For example, if the four component predictor values were all classified as “high”, the composite HSI state = high.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0098>.

Table 2. Node definitions and states for Bayesian belief networks to assess bull trout habitat and population vulnerability to wildfire in the Wenatchee River basin, Washington, USA.

Belief network	Node name	Definition	State
Habitat suitability	Gradient	Likelihood of bull trout occurrence in a stream reach as a function of percent gradient (GRAD)	Low (0–0.32); moderate (0.33–0.66); high (>0.66)
	Winter high-flow events (Scour likelihood)	Likelihood of bull trout occurrence as a function of mean. number of days in winter (Dec.–Mar.) that flow was in top 5% of annual flows (W95)	Low (0–0.32); moderate (0.33–0.66); high (>0.66)
	Maximum temperature (Water temperature)	Likelihood of bull trout occurrence as a function of maximum annual water temperature (TMAX)	Low (0–0.32); moderate (0.33–0.66); high (>0.66)
	Summer flow (Stream size)	Likelihood of bull trout occurrence as a function of mean summer (June–Sept.) stream flow (SFLOW)	Low (0–0.32); moderate (0.33–0.66); high (>0.66)
	Habitat suitability	Potential spawning and rearing habitat quality for bull trout based on reach gradient, winter high-flow events, maximum temperature, and summer flow (HSI)	Low, moderate, high
Vulnerability	Number of road crossings (Downstream road crossings)	Number of road crossings between focal reach and nearest downstream patch (ROADX)	None (0); few (1–5); some (5–14); many (≥15)
	Distance to nearest patch (Patch distance)	Distance from focal reach to nearest downstream patch (PATCHDIST)	Adjacent (<1 km); near (1–5 km); moderate (5–10 km); far (>10 km)
	Intervening passage	Combination of number of downstream road crossings and distance to nearest patch (INTERV)	Low, moderate, high
	Above barrier	Focal reach is upstream from an impassible barrier (ABVBAR)	Yes, no
	Recolonization potential	Potential for recolonization of focal reach from nearest patch based on intervening passage and above barrier (RECOL)	Low, moderate, high
	Postfire habitat size (Patch size)	Total stream length within focal patch with high HSI (>2.0; PATCHSIZE)	Small (0–7 km); medium (8–40 km); large (>40 km)
	Fire likelihood	Mean probability of a fire ignition within a focal reach contributing area (FIRELIK)	Low (0–0.25); moderate (0.26–0.50); high (>0.50)
	Postfire HSI change	Percent change in habitat suitability pre- to post-fire (ΔHSI)	Slight (0%–5%); moderate (5%–15%); high (>15%)
	Prefire habitat suitability	Percentage of reach with high HSI (>2.0; PREFIRE)	None (0%); low (1%–25%); moderate (26%–75%); high (>75%)
	Local habitat fire impact	Potential for fire effects for a focal reach based on fire likelihood, postfire habitat change, and prefire habitat suitability (LOCAL)	Low, moderate, high
	Vulnerability	Vulnerability of a focal reach to wildfire based on external recolonization potential, internal resistance, and local fire effects (VULN)	Low, moderate, high

Note: Node names in parentheses are provided to coincide with factors displayed in Fig. 3.

Conversely, if all four were “low”, HSI = low. For intermediate cases, we weighted the influence of the predictors according to their mean effect size (Table S1¹). For example, stream gradient (%) is consistently associated with bull trout occurrence, but effect size is small relative to other factors (Dunham and Rieman 1999; Dunham et al. 2003a; Wenger et al. 2011a). Mean effect size for the four predictors was interpreted from the published literature on bull trout – habitat relations (Dunham and Rieman 1999; Dunham et al. 2003a; Rich et al. 2003; Wenger et al. 2011a). The CPT for the HSI was based on these weights (Table S2¹).

Local effects of wildfires

We evaluated the potential effects of wildfires on habitat suitability as a function of the probability of wildfire occurrence within each RCA, using the same fire model as above, and an estimate of the postwildfire habitat change from the HSI model (hereafter ΔHSI). The probability and uncertainty of a wildfire being adjacent to any reach (FLEST) was estimated as the mean ($\mu_{f_{\text{like}}}$) and standard deviation ($\sigma_{f_{\text{like}}}^2$) of probable flame lengths from all simulated wildfires occurring in cells within each RCA polygon, respectively. Continuous values of FLEST were reclassified to the categorical values of low (0–0.25), moderate (0.26–0.50), and high (>0.50) (Table 1) using the formula

$$(2) \quad P(\text{FLEST} | \mu_{f_{\text{like}}}, \sigma_{f_{\text{like}}}^2) = N(x, \mu_{f_{\text{like}}}, \sigma_{f_{\text{like}}}^2)$$

The potential effect of wildfire on local bull trout habitats was assessed as postfire habitat change (ΔHSI), based on the relations between wildfire and changes in LST, and the predictive relationship between LST and stream temperature, as described above. Gradient, stream size, and winter stream flows were assumed to be independent of wildfire. The ΔHSI from pre- to post-fire conditions was calculated every 200 m along a reach as the proportion $(\text{HSI}_{\text{pre}} - \text{HSI}_{\text{post}}) / \text{HSI}_{\text{pre}}$. This value was then averaged across each reach ($\mu_{\Delta\text{HSI}}$), and the SD of that mean was calculated ($\sigma_{\Delta\text{HSI}}^2$). In the model, ΔHSI (range: 0–1) was estimated for each reach as

$$(3) \quad P(\Delta\text{HSI} | \mu_{\Delta\text{HSI}}, \sigma_{\Delta\text{HSI}}^2) = N(x, \mu_{\Delta\text{HSI}}, \sigma_{\Delta\text{HSI}}^2)$$

Continuous values of ΔHSI were reclassified to categorical values of low (0.00–0.05), moderate (0.06–0.15), and high (>0.15).

With information on the probability of a wildfire and the potential ΔHSI, we were able to modify the prefire HSI (coded as PREFIRE in the BN) to predict local effects of wildfire. We added a

node to remove the potential occurrence of the nonsensical case of a reach with low prefire HSI being ranked as highly vulnerable, owing to a relatively large Δ HSI. To do so, we calculated the proportion of 200 m points within a given reach predicted to be in the high HSI state, where PREFIRE states were as follows: none = 0.00, low = 0.01–0.25, moderate = 0.26–0.75, or high > 0.75 (Table 2). The “local effects of fire” node (LOCAL) CPT (Table S3¹) was parameterized so that reaches with low potential wildfire effects had a low likelihood of fire, and little expected change from pre- to post-fire conditions (i.e., fire severity was low), and there was little or no high-quality habitat present under prefire conditions.

Connectivity

Vulnerability of bull trout populations to wildfires is partially conditioned by habitat connectivity and resistance to fish movement (Rieman et al. 1997; Dunham et al. 2003b). In our BN, we evaluated connectivity between habitat patches as the potential for any reach to be recolonized by fish (RECOL) from another patch. Connectivity was highest where impassible barriers were absent, where no road crossings were present along the shortest interpatch route, and where the distance (km) to the nearest patch was short.

To directly characterize barriers, we relied on a State of Washington spatial database (StreamNet 2012; http://www.streamnet.org/mapping_apps.cfm; Fig. 1) of man-made dam, culvert, waterfall, and gradient barrier (e.g., cascades) locations. Reaches upstream of a barrier were given a binary descriptor (0 = not above a barrier, 1 = above a barrier). In the BN model, the ABVBAR node (states = yes or no) indicated whether a reach was above a barrier.

Because stream–road crossings often form partial to complete fish passage barriers (GAO 2001), we also evaluated stream–road crossings in the connectivity section of the BN model. Using a digital road layer for the entire basin (<http://www.fs.fed.us/r6/data-library/gis/okanogan/index.shtml>) and a custom C++ script (available on request), we identified all road crossings, and summed the number between a focal reach and the outlet of the nearest patch, along the minimum in-stream distance (ROADX). In the model, states for the ROADX node were none (0 crossings), few (1–5 crossings), some (6–14 crossings), and many (≥ 15 crossings).

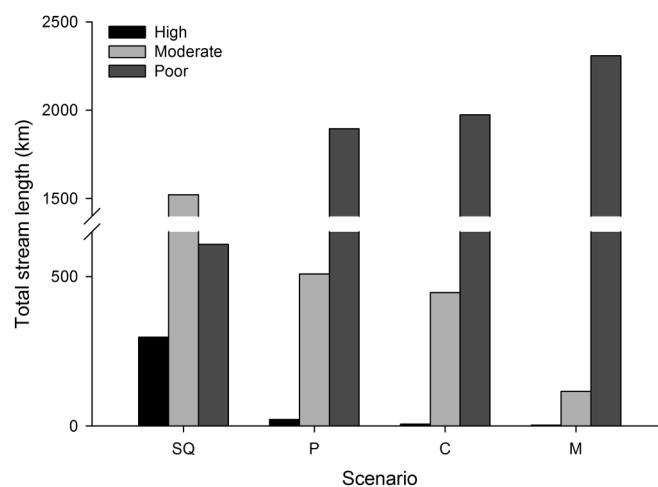
In addition to measures of local resistance to movement (i.e., complete and partial barriers), we also considered movement distance, expressed as the stream length between a given focal reach and the nearest occupied patch. We used a custom C++ script (available on request) to calculate the minimum in-stream distance (PATCHDIST; km) from each stream reach to the nearest patch outlet (i.e., pour point). We assumed this measure was an adequate proxy for the influence of terrain dissection on the potential for recolonization and persistence (occurrence, Dunham and Rieman 1999). In the model, we reclassified continuous values of PATCHDIST into categorical values using the stratification schema reported in Dunham and Rieman (1999; Fig. 5): adjacent (< 0.01 km), near (0.01–4.99 km), moderate (5.00–9.99 km), and far (≥ 10.00 km). In the BN, we created an intermediate node to represent intervening passage (INTERV; Table S4¹) between a focal reach and the nearest patch that incorporated ROADX and PATCHDIST.

The “recolonization potential” node represented the potential for a focal stream reach to be recolonized (RECOL) from another patch as a function of whether the reach was located above an impassible barrier (ABVBAR) and the potential for movement among patches (INTERV). We weighted the effects of isolation by barriers (ABVBAR = yes) more heavily than those of the combined effects of PATCHDIST and ROADX (Table S5¹).

Patch size

Existing information suggests that bull trout persistence is most strongly linked to the size of coldwater patches (Rieman and McIntyre 1995; Dunham and Rieman 1999). Large habitats support larger populations than smaller habitats, which in turn should

Fig. 5. Total stream length in the Wenatchee River basin, Washington, USA, classified to three bull trout spawning and rearing habitat suitability classes under the status quo (SQ) and three climate scenarios: P, low warming; C, moderate warming; M, high warming.



afford increased resistance to extinction, because localized disturbances are less likely to affect an entire population (Dunham et al. 2003b). Based on results of the HSI model, we calculated bull trout habitat “area” (km²) as the total prefire stream length in a patch that was categorized as high-quality spawning and rearing habitat. We then compared habitat area in a patch to the median wildfire size in the study basin (~1100 ha; Fig. 2). Because wildfire size was measured in hectares and bull trout habitat in kilometres, we converted length to area by calculating the mean stream density (km·ha⁻¹) for patches in the Wenatchee Basin based on the NHD hydrography layer. This resulted in a 0.007 km·ha⁻¹ conversion factor. In the BN, we considered a patch to be highly vulnerable to extirpation when its patch size (PATCHSIZE) was at or below the median fire size. We reclassified continuous values of PATCHSIZE into the categorical values as follows: small, ≤ 7 km; medium, 7–40 km; and large, >40 km.

Vulnerability

The final node in our BN represented the combined effects of fire on local habitat suitability (LOCAL), recolonization potential of focal reaches by bull trout postfire (RECOL), and the likelihood of recolonization from within a patch postfire, represented by patch size (PATCHSIZE). To parameterize the CPT table we used the following rationale. We considered PATCHSIZE and RECOL to be the most important factors influencing the vulnerability of bull trout populations postfire, followed by LOCAL, which we considered to be relatively less important (Table S6¹). For example, even if the likely effects of a fire on a focal reach were high, and if the patch that contains the reach is large relative to the median fire size, and the potential for recolonization is high (the contributing reach is not above a barrier), the focal reach is likely to be recolonized once suitable habitat conditions return, and thus population vulnerability would be low. Conversely, even moderate impacts of fire on a focal reach located in a small, isolated patch would contribute towards that population being highly vulnerable to fire. We used this rationale to systematically populate the CPT table for bull trout population vulnerability to fire (Table S6¹).

Modeled scenarios

Our final objective was to contrast current bull trout vulnerability to wildfires across three climate change scenarios. To do so, we estimated the most probable state and associated uncertainty

Table 3. Matrix of climate change scenarios and management options contrasted for bull trout habitat and population vulnerability to wildfire in the Wenatchee River basin, Washington, USA.

Climate scenario	Management option			
	None	Increase connectivity	Decrease fire size	Both
SQ	x	x	0	0
P	x	x	x	x
C	x	x	x	x
M	x	x	x	x

Note: x, scenario conducted; 0, scenario not conducted. Status quo (SQ), low warming (P), moderate warming (C), and high warming (M) are shown.

for all reaches at each major node (RECOL, LOCAL, PATCHAREA, VULN) in the BN. We considered these to represent the “status quo” (SQ; reference year 2012) conditions or scenario. The three climate change scenarios were based on those developed by Wenger et al. (2011b) as part of a large-scale assessment of trout vulnerability to climate change in the intermountain West. Estimates were based on projected flow regimes downscaled from general circulation models (GCMs) simulating conditions in the 2040s under the A1B emissions scenario (Wenger et al. 2010). The three climate change scenarios used were high warming (CCM; MIROC3.2), low warming (CCP; PCM1), and a composite of 10 GCMs (CCC) to represent moderate warming. Because we did not have direct estimates of TMAX from these scenarios, we took a conservative approach and increased TMAX by 1, 2, and 3 °C uniformly across all stream reaches for the CCP, CCC, and CCM scenarios, respectively. These values are within the range of expected water temperature increases predicted for the western United States (Isaak et al. 2012), although we recognized that there is much local variation in stream temperature response to climate (Arismendi et al. 2012). We did not change GRAD for the climate change scenarios because it was an immutable geomorphic characteristic within the timescale of our study. Using future (2040s) estimates of SFLOW and W95 generated by Wenger et al. (2011b), and elevated TMAX values, we recalculated the HSI for each of the three climate scenarios. Within the model, we increased the median wildfire size from 1097 to 1370 ha (25%) as a conservative estimate of predicted wildfire size increases of 25%–50% by midcentury in the Pacific Northwest under climate change conditions (Hessl 2011).

Finally, we considered the effects of two climate adaptation actions to increase bull trout persistence likelihood in the face of climate change, including increasing population connectivity and (or) controlling wildfire (Table 3). At present, bull trout habitat in the Wenatchee River basin is highly fragmented, with numerous natural and man-made barriers. Key actions to increase connectivity are to remove barriers or translocate fish above barriers (e.g., Neraas and Spruell 2001). To simulate this first action, we set all reaches in the model to be “not above barrier” (ABVBAR = no) and applied this to all scenarios. The second management option was to maintain current wildfire size (1097 ha) via suppression or fuel management. We implemented this action in the BN by holding the current median wildfire size constant and rerunning the model for each of the three climate scenarios.

Model sensitivity

We assumed uniform prior probabilities and used the entropy reduction method supplied in the Netica software to test the influence of individual nodes on model results (Marcot et al. 2006). Sensitivity values were computed for the HSI and model nodes across the range of possible input conditions.

Table 4. Total length of stream (km) classified as high-quality bull trout spawning and rearing habitat within six subwatersheds in the Wenatchee River basin, Washington, USA.

Subwatersheds	Scenario			
	SQ	P	C	M
Chiwawa River	47.6	2.5	0.7	0.4
Chiwaukum Creek	13.1	0.0	0.0	0.0
Icicle Creek	99.2	4.3	1.2	0.6
Little Wenatchee River	47.3	22.2	4.3	2.2
Nason Creek	41.8	0.0	0.0	0.0
Peshastin Creek	3.3	0.0	0.0	0.0
White River	39.1	0.0	0.0	0.0

Note: Results are shown for current (2012) status quo (SQ) conditions and under three climate change scenarios (2050). See text for full description of scenarios.

Results

Status quo (SQ) scenario

Habitat suitability

Eleven patches were delineated based on the 17 °C cut-off (Fig. 4; Table 1). The number of patches within subwatersheds (i.e., 12-digit HUCs, NHD) ranged from 1 to 4. Under the SQ and across the Wenatchee River basin, a total of 297.3 km of high-quality bull trout spawning and rearing habitat was predicted by the model (HSI = high; Table 4; Fig. 5). The Icicle Creek subwatershed contained the most high-quality habitat (99.2 km); the Chiwawa River and Little Wenatchee River subwatersheds also contained abundant high-quality habitat (47.6 and 47.3 km, respectively). In general, high-quality habitats occurred at higher elevations and in more northerly parts of the basin. Chiwaukum Creek contained the fewest kilometres of high-quality habitat (13.1 km).

Local effects of wildfire

Predicted fire severity varied spatially across the basin with 43.5% (1500 km²), 51.0% (1760 km²), and 5.4% (186 km²) of the total area classified as low, moderate, and high severity, respectively. Across six of seven subwatersheds, the proportion of total land surface area classified as high severity was relatively consistent (mean = 0.069; SD = 0.004). Total high-severity pixels in Peshastin Creek was lower (0.035), owing to a preponderance of early seral and open-canopy forest conditions from prior logging.

The mean wildfire likelihood (μ_{flike}) ranged from 0.02 to 0.66 (mean \pm SD = 0.19 \pm 0.12) across all reaches in the basin. After accounting for variation within RCAs (σ_{flike}^2), 61.3% of reaches had FLEST (probability of a wildfire) classified as low, 31.4% as moderate, and 7.3% as high. The mean uncertainty associated with FLEST (FLEST_{SD}) ranged from 0.01 to 0.33 (mean \pm SD = 0.11 \pm 0.06), indicating considerable heterogeneity in wildfire likelihood and severity for a given reach. Icicle Creek contained the most stream reaches in the moderate and high FLEST categories (Table 5). Chiwaukum and Nason creeks also contained a number of reaches in the moderate category (40% and 29%, respectively).

Across the basin, where wildfires were predicted to occur, the relative change in habitat quality ($\mu_{\Delta\text{HSI}}$) from pre- to post-fire conditions ranged from -6.4% to -20.0% (mean \pm SD = 14.0 \pm 2.1), and the associated $\sigma_{\Delta\text{HSI}}^2$ ranged from 0.1 to 8.1 (mean \pm SD = 1.3 \pm 1.1). After incorporating parameter uncertainty, <4% of reaches were predicted to change slightly (0%–5%), 71.2% were predicted to change moderately (5%–15%), and 25.6% were expected to be highly impacted. Reaches with the largest $\mu_{\Delta\text{HSI}}$ were located at higher elevations, where intuitively TMAX would be colder and thus more suitable for bull trout occurrence.

Table 5. Total length (km) and proportion (in parentheses) of stream reaches classified to three states of fire likelihood and predicted postfire habitat change in seven subwatersheds in the Wenatchee River basin, Washington, USA.

Subwatersheds	Fire likelihood			Post-fire habitat change		
	Low (0.00–0.25)	Moderate (0.26–0.50)	High (>0.50)	Slight (0%–5%)	Moderate (6%–15%)	High (>16%)
Chiwawa River	241.43 (0.93)	15.28 (0.06)	2.77 (0.01)	0.00 (0.00)	8.82 (0.19)	38.80 (0.81)
Chiwaukum Creek	40.45 (0.60)	27.43 (0.40)	0.00 (0.00)	0.00 (0.00)	2.57 (0.20)	10.57 (0.80)
Icicle Creek	269.16 (0.80)	52.47 (0.16)	12.93 (0.04)	0.29 (0.00)	22.75 (0.23)	76.20 (0.77)
Little Wenatchee River	156.78 (0.75)	49.56 (0.24)	1.60 (0.01)	0.69 (0.01)	24.13 (0.51)	22.46 (0.47)
Nason Creek	121.39 (0.69)	50.83 (0.29)	3.20 (0.02)	0.00 (0.00)	5.49 (0.13)	36.35 (0.87)
Peshastin Creek	99.91 (0.81)	22.92 (0.19)	0.00 (0.00)	0.59 (0.18)	0.58 (0.18)	2.14 (0.65)
White River	154.04 (0.92)	13.37 (0.08)	0.00 (0.00)	0.00 (0.00)	5.07 (0.13)	34.00 (0.87)

Note: Lengths for habitat change are only for reaches classified as high-quality bull trout spawning and rearing habitat (see text for details).

Recolonization potential

Over half (876.2 km; 55%) of all reaches located within bull trout habitat patches in the basin were above an impassible barrier. The in-stream distance from one habitat reach to the nearest patch ranged from <1 to 62.6 km (mean \pm SD = 24.7 \pm 13.2). The majority (85.3%) of reaches were located >10 km from the nearest patch. On average, bull trout would traverse 6.7 road crossings to recolonize a focal reach from an adjacent patch, and only 7% of reaches had no road crossings between them and the nearest patch. Most (83.5%) reaches were located above 1–14 crossings, and 9.5% had >15 crossings between them and the nearest patch. The number of crossings ranged from 0 to 19 (mean \pm SD = 4.4 \pm 4.1).

Patch size

Under the SQ, 9 of 11 patches contained >7 km of high-quality spawning and rearing habitat, which were larger than the median regional wildfire size (Fig. 6). Four patches had >40 km classified as high quality (i.e., PATCHSIZE = large).

Vulnerability and uncertainty

Under the SQ scenario, 12.6, 417.7, and 907.5 stream km were classified as high, moderate, and low vulnerability, respectively (Fig. 7a); the majority classified as high or moderately vulnerable were located in Peshastin and Chiwaukum creeks, and the Little Wenatchee River (Fig. S2¹). Vulnerability rankings are useful, but quantifying the associated uncertainty of predictions is also important (Fig. S3¹). For example, although vulnerability to wildfire for most reaches in Icicle Creek was low, estimates showed higher associated uncertainty, indicating less support for the low-vulnerability finding. This was in direct contrast to results for the Chiwawa River, where vulnerability and uncertainty were predicted to be low.

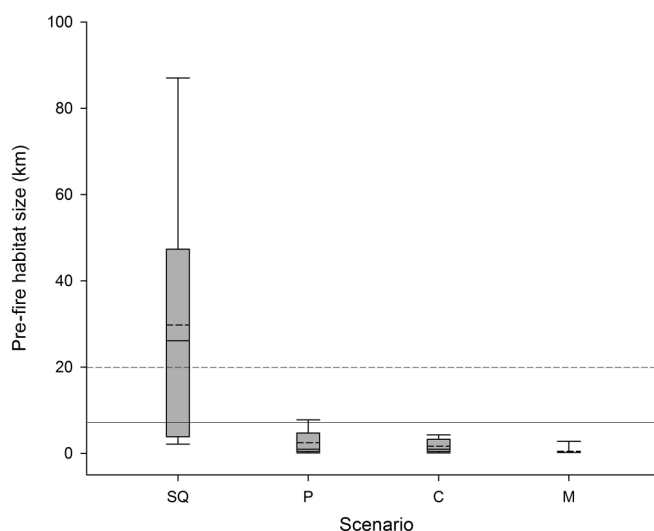
Climate change scenarios

Prewildfire stream length classified as highly suitable for bull trout was reduced by at least one order of magnitude under the three climate change scenarios (range 3.1–22.2 km) relative to the SQ scenario (297.3 km; Fig. 5). Less severe changes were predicted under the low (CCP) and moderate (CCC) warming scenarios. For example, over 500 km of moderately suitable habitat remained under the CCP scenario. These changes were driven primarily by increased TMAX and W95 (Fig. S4¹), although modest reduction in SFLOW was also predicted (Fig. S5¹).

Across the three climate change scenarios, no reaches were classified as having low vulnerability to wildfire, indicating that bull trout population susceptibility to wildfire effects stems from changes to physical habitat conditions and increased wildfire size (Fig. 7). Additionally, total habitat length was much reduced (i.e., reduced PATCHSIZE) owing to climate change effects (relative to the SQ scenario; Table 4).

Increasing connectivity had little effect on vulnerability under the SQ scenario because patches were generally large enough to

Fig. 6. Boxplots of total stream length classified as high-quality bull trout spawning and rearing habitat for 11 patches in the Wenatchee River basin, Washington, USA, under a status quo (SQ) and three future climate change scenarios: P, low warming; C, moderate warming; M, high warming. Within boxes, dashed lines represent the mean, solid line the median, and whiskers the 5th and 95th percentiles. Dashed and solid horizontal lines represent the mean and median regional fire sizes, respectively (see Fig. 2).



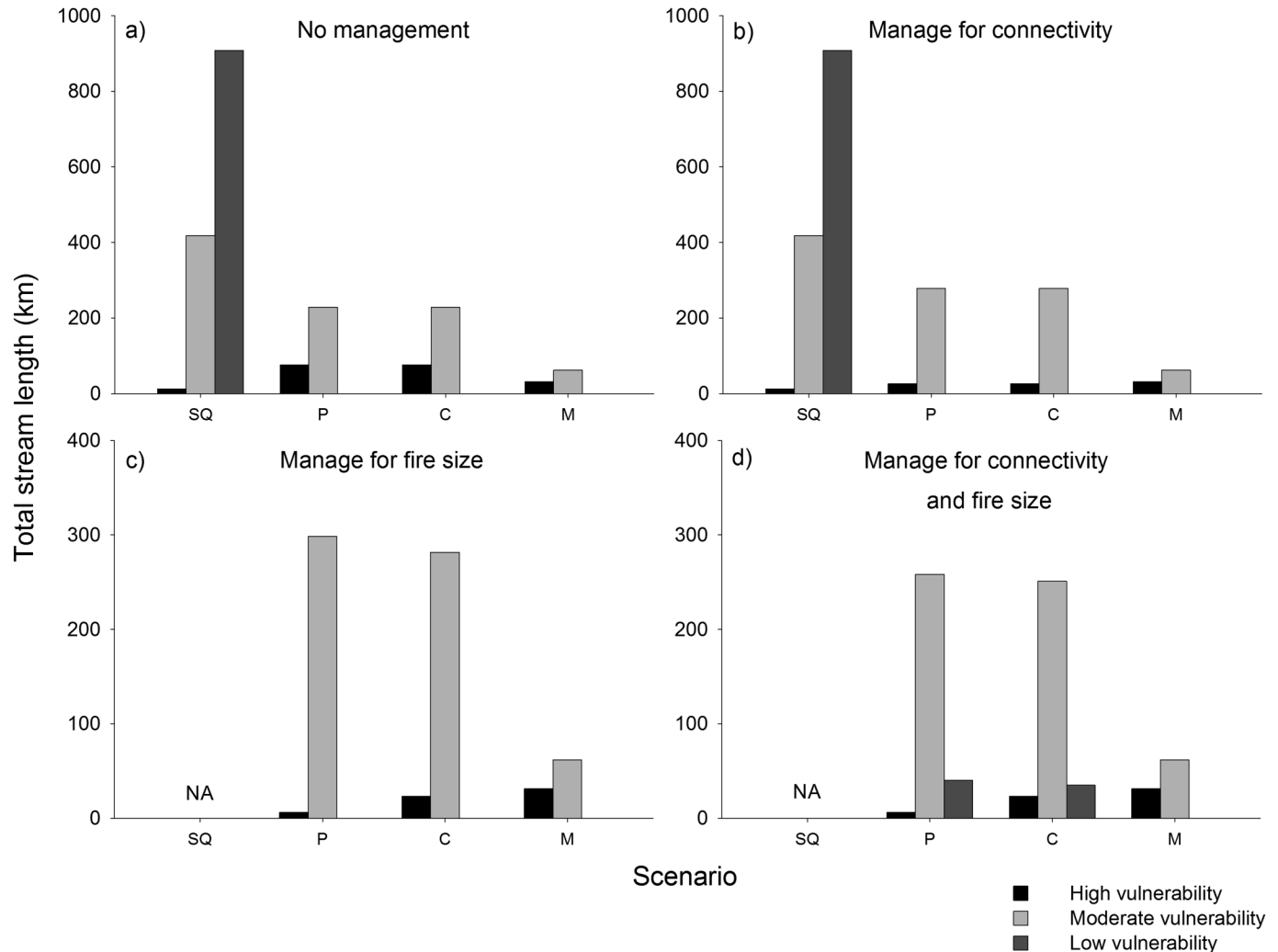
ensure internal recolonization following wildfire (Fig. 7b). There was a modest reduction in stream length classified as highly vulnerable across the CCP and CCC scenarios when connectivity was increased. Vulnerability remained much the same under the CCM (high warming) scenario, regardless of whether connectivity was increased.

Managing for reduced wildfire size reduced the length of streams classified as highly vulnerable to wildfire by 91% and 69% under the CCP and CCC scenarios, respectively (Fig. 7c). Under the CCM scenario, vulnerability remained the same regardless of fire management. In a scenario comparison, managing for enhanced connectivity and reduced wildfire size versus managing fire size alone resulted in there being no difference in highly vulnerable stream length, but with the former, stream length classified as low vulnerability increased (Fig. 7d). Under no climate change scenarios were any reaches classified as low vulnerability, indicating that employing multiple management options may be useful to enhance bull trout habitat suitability under a warming climate.

Sensitivity analysis

Both the HSI and BN behaved as expected given their structure and the variable weighting influences. In the HSI, bull trout

Fig. 7. Total stream length classified to three states of bull trout population vulnerability to wildfire under a status quo (SQ) and three climate change scenarios: P, low warming; C, moderate warming; M, high warming. Four management options are presented: no management (a), manage for connectivity (b), manage for fire size (c), and manage for both connectivity and fire size (d). See text for description of management options and scenarios.



habitat suitability was most sensitive to TMAX and its associated nodes (variance reduction = 0.469), followed by W95 (0.116), SFLOW (0.023), and GRAD (0.014). In the model, VULN was most sensitive to PATCH SIZE (0.367), followed by RECOL (0.022) and LOCAL (0.017), and their components.

Discussion

Although climate projections indicate major losses of suitable bull trout habitat throughout much of the species' range (e.g., Rieman et al. 2007; Isaak et al. 2012; Wenger et al. 2013), results which the current study supports, our analysis also shows that local management can significantly reduce the vulnerability of this species to climate change. Our findings also differ from a similar previous effort that considered winter flooding, summer low flows, and summer temperature influences on bull trout, in the context of managing nonnative brook trout and climate change impacts (Peterson et al. 2013). Our scenarios did not consider brook trout management, because earlier work did not detect an influence of brook trout on presence of bull trout in our study basin (Dunham et al. 2003a). However, we acknowledge that threats posed by brook trout may be important in other locations (Dunham et al. 2002).

Modeling results helped us to identify key habitat constraints and management opportunities useful to influencing bull trout persistence likelihood in the face of likely climatic and wildfire futures (sensu Rieman et al. 2010). Our findings are applicable to coarser-scale assessments of vulnerability for bull trout across the species' range (e.g., US Fish and Wildlife Service 2008), as well as for other salmonid species with similar habitat requirements. The results of this work, considered in the context of past bull trout and climate evaluations, show that bull trout vulnerability to climate change depends on (i) the extent to which effects can be offset by management, (ii) how other cofactors can be managed or mitigated, and (iii) the magnitude of climate change itself. We discuss each of these three themes below along with future research and management needs.

Wildfire can have an impact on salmonids in streams. In particular, episodic, high-magnitude disturbances (e.g., extreme flooding, debris flows) within days to the first few years following a severe wildfire (Miller et al. 2003; Wondzell and King 2003) can lead to local extirpations (Dunham et al. 2003b). Over the longer term, fire-related changes in channel form and, most importantly, temperatures, can lead to changes in riverine food webs (Minshall 2003; Rosenberger et al. 2011; Davis et al. 2013), a host of temperature-

linked physiological effects on fish (Jager et al. 1999), and ultimately mortality or local extirpation if temperatures exceed lethal limits. However, given sufficient connectivity, salmonids can recover quickly from wildfire (Rieman et al. 1997; Burton 2005; Dunham et al. 2007; Neville et al. 2009) if suitable environmental conditions exist. Moreover, alteration of physical habitat from debris flows and landslides following wildfire may result in the extirpation of nonnative species and a concurrent colonization of native species (Sestrich et al. 2010).

We assumed that the availability of suitably cold habitats relative to the mean area of wildfires provided an indication of relative vulnerability, and that larger and more severe fires can drastically reduce suitable habitat and vulnerability to extinction. However, we did note that in the absence of management, habitat size declined more dramatically (Fig. 6), resulting in substantially increased vulnerability of bull trout populations (Fig. 7). Although much of the Wenatchee River basin is affected by barriers to fish movement, managing for increased connectivity had little influence on bull trout vulnerability to climate change (Fig. 7). In contrast, management to reduce fire size greatly improved the future outlook for bull trout, although less so for the most pessimistic climate scenario. These findings suggest that there are management opportunities for improving bull trout resilience to climate change, and that some actions (e.g., fire management) may be more important than others (e.g., managing nonnative brook trout or connectivity).

Although climate can pose serious threats to bull trout (e.g., Table 4), our results suggest that local actions such as barrier removal or fuel management can be effective in reducing vulnerability in the face of climate change (e.g., Fig. 7). Furthermore, the actions we considered are among those already in place or part of long-term management prescriptions for bull trout (e.g., US Fish and Wildlife Service 2008), and more generally (Littell et al. 2011) across the region. Obviously, questions remain regarding whether sufficient resources can be directed to implementing management in a timely manner, but for bull trout in the Wenatchee River basin, focused actions with limited resources will likely provide benefits.

The Wenatchee River basin likely represents a unique setting and configuration of threats, but many of the fundamental processes we modeled are in operation across the range of bull trout, and lessons learned from our applications may be useful in other locations. Analyses in other locations may identify different threats and associated management actions. For example, threats from debris flows immediately following fire (Lyon and O'Connor 2008) or nonnative brook trout may be more important in other locations (e.g., Leary et al. 1993; Kanda et al. 2002; DeHaan et al. 2010). In studies of other salmonids, threats from loss of connectivity and hybridization with nonnative species have proven to be more important than the threat of wildfire in the short term (Neville et al. 2009; Neville and Dunham 2011). As with this study, our collective view of threats may change over time. For example, negative impacts of climate change on nonnative species may indirectly benefit native species (Wenger et al. 2011a).

Given the complexity of factors at play, it is difficult to translate any scenario analysis into absolute predictions of local outcomes. For example, recent work shows that historical changes in stream temperatures do not always track atmospheric changes (Arismendi et al. 2012). Many localized factors are known to influence both hydrological and thermal characteristics of streams (e.g., Safeeq et al. 2013), including those associated with land management (Moore et al. 2005). The approach we have developed here is useful to applying regional climatic projections to watershed vulnerability assessments, but we suggest that realization of climate-related changes in streams will strongly depend on local conditions.

Over longer time periods and more extreme change projections it is plausible that climate impacts can overwhelm our capacity to locally adapt. Furthermore, recent work has shown that uncer-

tainty regarding the future climate may be more important than our uncertainty with how bull trout will respond to the climate (upper Columbia River basin; Wenger et al. 2013). Accordingly, where climate change impacts are predicted to be more extreme than those considered here, broad-scale management alternatives, such as restoration of riparian zones (Cristea and Burges 2010), may be more effective. Such actions may occur at much larger scales than those normally considered in land and species management plans, and may include wholesale translocations (Hulme 2005; Thomas 2011) or conservation efforts in new parts of species' ranges (Peters 1988).

Our habitat suitability model focused on bull trout spawning and rearing habitats. Similar to other salmonids, bull trout display a diversity of life histories, including smaller-bodied stream residents and large-bodied fluvial-migratory life histories (Dunham et al. 2008), the latter of which are likely reduced in abundance in the Wenatchee River basin owing to extensive habitat fragmentation and degradation in lower mainstem reaches, which were not included in our model. To apply our model to basins with a significant migratory bull trout component, nodes that characterize large river rearing or refuge habitat could be included.

Although our HSI was based on empirical models that have successfully predicted bull trout occurrence in other basins, owing to the listed status, distribution data specific to the Wenatchee River basin are limited. However, of the 21 georeferenced observations of adult or juvenile bull trout available (J. Falke, unpublished data), all fell within reaches that our HSI index predicted to be high-quality habitat. Moreover, reaches designated as critical habitat within the study basin (US Fish and Wildlife Service 2008) aligned well with predicted habitat suitability. Range-wide critical habitat maps based on expert opinion are available for this species and could be incorporated to supplement BN model predictions.

We predicted fire severity and likelihood in the Wenatchee River basin using a state of the art, spatially explicit fire growth model parameterized to reflect local topography and fuels. For our future climate and management scenarios, we assumed that fire size would increase by 25%, but we held severity and likelihood constant. This assumption is conservative in light of some climate forecasts, particularly those extending over longer (>30 year) time horizons. However, resilience and percolation theory indicate that fire severity and size do not inexorably increase (Stauffer and Aharony 1991). Postfire changes in vegetation can influence the frequency, size, and severity of subsequent fires (see Moritz et al. 2011 and references therein). This is more likely after about 40%–50% of the landscape has burned. For this reason, we took a conservative approach in estimating future fire size and severity under climate change scenarios. Given that our confidence in any prediction or projection decreases as the time horizon increases, we opted to focus on a relatively short (30 year) period, reasoning that our understanding of future scenarios is bound to improve dramatically in coming decades and that trends in the next 30 years are nonetheless relevant to climate adaptation and other management objectives. Moreover, near-term forecasts are most applicable to current managers, because scenarios made under these time horizons (years to decades) will effectively need to be considered during their tenure (Carpenter 2002).

Subsequent studies of future fire effects on native fishes should incorporate scenarios that represent expected vegetation change via state-transition models that directly incorporate vegetation and disturbance dynamics (e.g., see Keane et al. 2008; Scheller et al. 2007). Using our BN and climate scenario modeling approach, fish population vulnerability could then be evaluated based on realistic future vegetation scenarios that include ongoing vegetation succession and disturbance, forest management, and their inherent variability, which may be more influential than factors already considered. In a modeling system employing state-transition modeling, forest management could be spatially

allocated opportunistically to prevent large and severe wildfires. Moreover, such modeling might create common ground between aquatic and terrestrial ecosystem managers and contribute towards a better understanding of how forests might be managed to benefit terrestrial and aquatic organisms (see Rieman et al. 2000, 2010).

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