

DISSERTATION

VULNERABILITY OF COLD-WATER AND COOL-WATER FISHES TO CLIMATE  
CHANGE WITHIN AN ANTHROPOGENIC CONTEXT USING BOOSTED REGRESSION  
TREES, DECISION SCALING, AND ECOSYSTEM SERVICES

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## ABSTRACT

### VULNERABILITY OF COLD-WATER AND COOL-WATER FISHES TO CLIMATE CHANGE WITHIN AN ANTHROPOGENIC CONTEXT USING BOOSTED REGRESSION TREES, DECISION SCALING, AND ECOSYSTEM SERVICES

Across the globe, environmental changes are occurring in ways that are profoundly important for freshwater ecosystems with implications for the occurrence of species. Typically, ecologists have sought to understand the distribution of freshwater species using natural environmental gradients. However, because rivers and streams embody a wide range of conditions due to human activity, adequately characterizing modern day drivers of species occurrence requires assessing both natural and anthropogenic influences within the context of global change. In recent decades, growing concerns over climate change have further contributed to the need to assess contemporary drivers of species occurrence. Despite this urgency, forecasting ecological responses to climate change remains a key conservation challenge. The aims of my research were to: a) investigate the drivers of western US riverine fish species occurrence within the context of global change; and b) project range-wide and site-level vulnerability of cold-water fish species to climate-induced changes in stream temperature and streamflow and to alternative land use trajectories.

In my assessment of contemporary drivers of cold-water and cool-water fish species distribution, I found that primary determinants of fish occurrence included human influences that accounted for a substantial portion of modeled outcomes among species. Sedimentation and nutrient enrichment were the two primary disturbance pathways by which human activities

influence aspects of stream condition that drive patterns of species occurrence. I also found that species had variable responses across anthropogenic gradients, suggesting that future efforts to characterize species-environment relations consider approaches that can capture nonlinear and threshold responses that occur along continuous gradients.

In a second analysis, I evaluated the range-wide vulnerability of cold-water fish species to projected climate change in the western United States and assessed site-level vulnerability to varying degrees of exposure to climate change and additional environmental stressors. I focused on rainbow trout (*Oncorhynchus mykiss* sp.) and cutthroat trout (*Oncorhynchus clarkii* sp.) -- two wide-ranging salmonids of significant conservation and economic importance. Using high resolution data on future stream temperature and mean annual flow, I projected climate-induced changes in suitable habitat across the historic native ranges of both species within the western United States. Projected declines in suitable habitat for cutthroat trout were substantial by 2080 and exceeded those of rainbow trout. A sensitivity analysis revealed that stream temperature warming was the primary driver of habitat loss for both species. Both cutthroat trout and rainbow trout exhibited regional variability in habitat loss that was consistent with the magnitude of projected warming for summer stream temperature. Cutthroat trout distributions are expected to shift upwards along an elevational gradient with warming causing fragmentation of contiguous habitat that will likely expose them to additional environmental disturbances. I conducted a complementary set of analyses using a decision-scaling approach to explore site-level vulnerability as a function of feasible climate futures and human-influenced environmental factors that have previously been implicated as key components of suitable habitat for cutthroat and rainbow trout. I uncovered important insights into species vulnerability including differential sensitivity to stream temperature warming among cutthroat trout and rainbow trout as well as

predominant influences of land use on species vulnerability independent of climate. Under a hypothetical climate adaptation scenario, I found that increased riparian cover shifted the distribution of vulnerability of cutthroat trout towards less frequent extirpations and that these benefits were achieved throughout feasible climate space. My findings suggest that augmentation of riparian vegetation is likely to be a robust climate adaptation strategy in an uncertain future. I conclude by offering two complementary approaches for advancing climate adaptation for freshwater systems in the face of uncertainty.

I also conducted a systematic review of hydrologic ecosystem services (HES) studies published within the past decade, finding compelling evidence that variability in methods used to quantify HES reflects an orientation towards decision making. I discuss implications of my findings on climate change vulnerability and consider ways to integrate an ecosystem services approach into the management and conservation of freshwater fish.

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## **1 Introduction**

The world is changing at unprecedented rates in ways that affect freshwater resources with consequences for human well-being and the distribution of species. Central to understanding both the drivers and implications of global change are connections linking people and organisms to the environment. Many of today's pressing environmental challenges -- climate change, habitat loss and fragmentation resulting from human transformation of the environment including land use change and hydrologic alteration of rivers, overexploitation, and the introduction of nonnative species -- will require multi-faceted solutions.

Ecology has much to offer towards sustainable management of freshwater systems that will also depend on integration of social and economic dimensions. As a Fellow of the I-WATER IGERT program sponsored by the National Science Foundation, I gained exposure to the type of approach that will be needed to confront contemporary issues related to freshwater resources. In many cases, it will take ecologists, hydrologists, engineers, climatologists, social scientists, and experts from other disciplines working together to appropriately formulate the problem and to investigate solutions. An overarching theme of my research is the role of human activities in shaping freshwater systems. This perspective is increasingly needed because the two are inextricably linked. Understanding these linkages will be key towards advancement of freshwater ecology and conservation.

Connections between people and the environment have been critical throughout human history. As a field, ecosystem services focuses on these connections, drawing explicit linkages between ecological systems and aspects of human well-being (MA, 2005). Advances in technology and scientific understanding have enabled the mapping and quantification of ecosystem services and have fostered greater awareness of the value of natural systems that

produce tangible benefits like clean air and clean water, regulate climate and disturbances, and pollinate crops (de Groot *et al.*, 2002). Mapping and quantification of ecosystem services is an essential part of the process linking ecosystem service research with decision making and has substantial influence over the quality and type of information that may be conveyed in a study.

Emerging contexts for decision making surrounding freshwater resources cover a diverse spectrum of issues, suggesting that there may not be a consistent need for the same types of information across studies. At the same time, a plethora of methods to map and quantify hydrologic (i.e. those relating to freshwater) ecosystem services (HES) have been implemented in studies with no clear blueprint for gauging their relevance. To assess these emerging decision contexts and to evaluate the application of disparate methods for mapping and quantifying hydrologic services, I performed a systematic literature review of peer-reviewed hydrologic ecosystem service studies published within the past decade. I evaluated each study ( $n = 49$ ) according to multiple dimensions of its decision context and analyzed in detail the methods used for quantification using multiple criteria for credibility, legitimacy, and saliency. I found compelling evidence that much of the variability in the quantification of HES can be explained by research motivations and scoping, reflecting the decision-oriented framing of the ecosystem services concept. The review of hydrologic ecosystem services highlights key knowledge gaps in the state of the science including the need to articulate beneficiaries and to make connections to policy and management more explicit.

Human alterations to the landscape exert influence over freshwater systems with consequences for the occurrence of species. Assessment of contemporary drivers of fish species distributions that include anthropogenic influences is key to understanding how current patterns of species occurrence fit within the broader context of human activities. In recent decades,

growing concerns over climate change have further contributed to the need to assess changes to climatic and environmental drivers of species occurrence. Despite this urgency, predicting ecological responses to climate change remains a key conservation challenge (Olden *et al.*, 2010) with difficulties posed by nonlinearities (Pilière *et al.*, 2014) and interactions among multiple drivers that include human pressures (Townsend, Uhlmann & Matthaei, 2008; Nelson *et al.*, 2009a; Palmer *et al.*, 2009; Kuemmerlen *et al.*, 2015). As evidence continues to mount of the diverse ways in which human activities influence flowing waters (Graf, 1999; Allan, 2004; Palmer *et al.*, 2008; Vorosmarty *et al.*, 2010), modeling efforts that can disentangle the role of environmental drivers (Pilière *et al.*, 2014) and project changes in species' distributions as a result of human activities are becoming increasingly relevant to management and conservation issues (Steen, Wiley & Schaeffer, 2010). I developed species distribution models (SDMs) using field-based and remotely sensed data to predict the occurrence of cold- and cool-water fishes across the western US. Following Allan (2004), I sought to establish mechanistic linkages between human activities and stream conditions that would directly influence fish occurrence, in order to support ecological interpretation of human influence.

Freshwater ecosystems are among the most imperiled worldwide with species facing disproportionate risk of extinction compared to other forms of biodiversity (Ricciardi & Rasmussen, 1999; Strayer & Dudgeon, 2010). Assessing changes to the distribution of freshwater fishes has become a priority area for research and conservation (Olden *et al.*, 2010) since stream organisms are considered uniquely vulnerable to climate change (Buisson *et al.*, 2008; Isaak & Rieman, 2013) and are threatened by numerous additional human stressors (Dudgeon *et al.*, 2006) including habitat fragmentation (Nilsson *et al.*, 2005) that is likely to limit opportunities for dispersal in a changing environment (Woodward, Perkins & Brown,

2010). Quantifying this vulnerability, however, presents a major challenge given inherent difficulty in modeling of climate projections and species response (Poff, Olden & Strayer, 2012) and the need to account for additional environmental influences that are likely to shape local responses (Isaak *et al.*, 2012). Fish species have frequently served as model organisms for understanding the effects of climate change on freshwater ecosystems with many foundational studies relying on established thermal tolerances as a way to assess impacts of a warming climate (Eaton & Scheller, 1996; Keleher & Rahel, 1996; Mohseni, Stefan & Eaton, 2003). Accurate assessment of thermally suitable habitat is essential for projecting species response to climate change (Caissie, 2006; Ficklin *et al.*, 2014) and has been limited in most broad-scale studies that have relied on crude approximations of warming.

Most studies of projected shifts in fish distributions have considered climate to be a key global change driver of fish species response and have evaluated future effects largely independent of non-climatic stressors (Comte *et al.*, 2013; Matthaei & Lange, 2015). However, knowledge of interactive effects between climate and other environmental stressors is increasingly needed to support climate adaptation and freshwater management in contexts that must also contend with these legitimate additional pressures (Domisch *et al.*, 2015; Kuemmerlen *et al.*, 2015). Given the ubiquitous transformation of the natural landscape and river systems by human activities (Allan & Castillo, 2007), and impending yet uncertain climate change, there is a need for studies that can assess vulnerability over a wide range of environmental conditions and can establish linkages to climate adaptation to support management in the face of uncertainty. I conducted a suite of analyses to model range-wide vulnerability of native salmonid species to projected stream temperature and streamflow in the western United States for 2040 and 2080. Recognizing that climate change projections remain uncertain, particularly with respect to

hydrology, and are likely to interact with additional stressors, I conducted a complementary set of analyses using a decision-scaling approach to explore vulnerability for plausible climate and land use futures while addressing uncertainty in modeled climate projections (Brown *et al.*, 2011). In this second set of analyses, I focused on a subset of sites representative of natural and anthropogenic gradients that exist in the western United States to examine vulnerability across scenarios for key stressors and climate adaptation strategies.

I applied many of the principles I distilled from the ecosystem services literature review into my subsequent analyses involving freshwater fish. For example, uncertainty surrounding climate projections and its impact to freshwater systems has been cited as a hindrance towards progress in climate adaptation. My use of a decision-scaling approach to explore how ecological vulnerabilities vary throughout potentially diverse climate and land use futures was intended to be decision relevant in the sense that it depicted plausibly variable outcomes that can be expected under alternative global change trajectories. Moreover, my investigation of potential benefits of riparian restoration to salmonid persistence was also salient to climate adaptation and management needs that include identification of robust climate change strategies. In addition, I discuss management implications of my research and of other studies, and communicate the need to consider multiple ecosystem services benefits in addition to maintenance of fish habitat as a viable conservation strategy moving forward.

I present the dissertation in three distinct chapters. Chapter 2 is published and appears in the *International Journal of Biodiversity Science, Ecosystem Services & Management* and includes David Theobald and Josh Goldstein as co-authors. N. LeRoy Poff and David Theobald are co-authors on Chapter 3, which is intended for submission to *Freshwater Biology*. David

Theobald and N. LeRoy Poff are co-authors on Chapter 4, which is intended for submission to Global Change Biology.

## **2 A systematic review of approaches to quantify hydrologic ecosystem services to inform decision making**

### **2.1. Introduction**

Interest from scientists in the concept of ecosystem goods and services (ES) has grown tremendously since the Millennium Ecosystem Assessment (MA) popularized the notion that ecosystems provide myriad benefits supporting human well-being (MA, 2005). The rise of ES science parallels the growing interest of actors in management and policy arenas to consider ES in their decision-making processes – a trend that has been reflected, for example, by recent implementation of high-level policy directives in Europe (e.g., the Blueprint to Safeguard Europe’s Water Resources; European Commission, 2012) and the United States (e.g., Incorporating Ecosystem Services into Federal Decision Making; Donovan *et al.*, 2015). The interface between ES science and decision making is particularly evident in the realm of freshwater resources, where hydrologic ecosystem services (HES) such as water supply, flood mitigation, and sediment regulation are important objectives (Brauman *et al.*, 2007; Allen, 2012). Demand for HES management is increasing, as evidenced at local levels by the proliferation of investments in watershed services (Bennett & Carroll, 2014) and more broadly through Federal policy developments (e.g., United States’ Principles and Requirements for Federal Investment in Water Resources; CEQ, 2013). These contexts for management collectively orient the field of HES towards decision making, establishing opportunities and a growing need for actionable science that can inform policy, planning, and management.

Hydrologic ecosystem services refer to the effects that terrestrial ecosystems have on freshwater (Brauman *et al.*, 2007). As such, a critical task for HES science is to understand how changes in the terrestrial environment (e.g., land use and land cover) and within river networks

(e.g., dams) affect benefits that range from sediment retention to hydropower generation (Postel & Thompson, 2005; Guswa *et al.*, 2014). A variety of methods have been used to quantify HES benefits (Brauman, 2015), and despite the availability of a substantial body of literature from which to draw inference, guidance for HES researchers to effectively engage in decision-relevant science is still evolving rapidly.

Recent reviews offer insight into the state of ES science more broadly. For example, Seppelt *et al.* (2011) examined 153 regional-scale studies, finding key methodological differences and limited use of validation procedures. Martinez-Harms & Balvanera (2012) reviewed 41 studies that mapped ES supply using social-ecological data and found that the quality of ES estimates varied substantially with method. Furthermore, they reported that the majority of studies did not validate results. Bagstad *et al.* (2013a) compared ES-specific tools and methods for a test region, documenting technical differences and tradeoffs among approaches. Crossman *et al.* (2013) advanced a framework for organizing ES research and used it to review 113 studies and suggested that protocols are needed to reduce the uncertainty of ES quantification and to mainstream methods to inform policy decisions.

From these reviews come two major findings. The first is that ES are not quantified using standardized methods, meaning that results obtained from different methods are generally not directly comparable. Furthermore, this situation limits opportunities to synthesize information across studies (Seppelt *et al.*, 2011; Liss *et al.*, 2013). These methodological inconsistencies have been recognized as potential setbacks for ES research (Seppelt *et al.*, 2011; Crossman *et al.*, 2013; Liss *et al.*, 2013). A second finding concerns the quality of published information. Methods are not equally credible and in many cases their estimates have not been tested against independent data despite known limitations of proxy data (Eigenbrod *et al.*, 2010).



A key challenge in operationalizing ES for decision making relates to the diverse settings in which research is called upon to inform decisions. To have an impact, approaches to quantify ES must resonate with decision makers whose needs vary with context (Ruckelshaus *et al.*, 2013). However, the needs of decision makers extend beyond quantifying and mapping ES and include qualities that have not received the same analysis in published ES reviews. For example, knowledge of the transparency of a study can be used to gauge its acceptability to stakeholders and decision makers (McNie, 2007; Nelson *et al.*, 2009).

In contrast to our understanding of methods for analyzing ES, considerably less is known about contexts for ES research including the types of decisions for which studies have been implemented. A broader understanding of ES science that encompasses these types of social considerations as well as technical aspects is needed to better integrate science into decision making (Rosenthal *et al.*, 2015). This would involve defining characteristic contexts for research and evaluating case studies within that framework.

The incorporation of ES criteria into a growing number of environmental policy and management settings provides an opportunity to evaluate advancements in the science and its application. Here, we aim to document the state of peer-reviewed ES science and to explore the characteristics of analyses conducted in different contexts for decision making, focusing specifically on HES for their policy and management relevance. To more deeply investigate the use of disparate methods and variable information content identified in previous reviews within the context of decision making, we addressed the following research questions: (1) *What are the decision-making contexts represented in peer-reviewed HES research?* and (2) *How do analytical approaches used to quantify HES benefits and changes in HES flows relate to quality of information, and how does this vary among decision contexts?* Based upon our findings, we

advance a framework for linking science to decision making for HES and provide new insights for researchers to expand the relevance of their work.

## **2.2. Literature review methodology**

We identified peer-reviewed publications using an ISI Web of Science search on quantitative ES assessments published between 2003 and 2013. We found that 560 journal articles met our search criteria of a hydrology-themed title (water\* OR hydro\* OR freshwater OR flood\* OR erosion OR multiple), ecosystem service topic (ecosystem service\* OR ecological service\*), and quantitative keywords (model\* OR quantif\* or map\* OR valu\* OR assess\*).

From this initial body of articles, we selected relevant literature by sequentially excluding papers based on title, abstract, and body (Pullin & Stewart, 2006). We then reduced this set of papers by excluding studies that did not explicitly quantify “the *benefits* people obtain from ecosystems” (i.e., ecosystem services) (MA, 2005); and map at least one aspect of ES (i.e., ecological inputs, supply, demand) (Crossman *et al.*, 2013). We focused on studies that used spatially-explicit methods, because maps are a critical tool for engaging stakeholders and communicating with decision makers (Daily, 2000; Naidoo & Ricketts, 2006; Palomo *et al.*, 2013).

We retained only those articles that expressed results in terms of a benefit to people as opposed to a purely biophysical endpoint. For example, a study that reported the avoided delivery of sediment to a reservoir was considered to quantify HES because it demonstrates a potential benefit for reservoir operators (i.e., the beneficiary). Conversely, a study that strictly modeled soil loss without relating its consequences to beneficiaries was rejected.

Table 2-1. Contexts for HES research, organized by key motivations (from Fisher *et al.*, 2009) and project scope (from Knight *et al.*, 2006). Case studies correspond to a single phase; however, ES studies may proceed through all phases over time.

		<b>Scope</b>		
		<i>Assessment</i>	→ <i>Planning</i>	→ <i>Management</i>
<b>Motivation</b>	<i>Understanding and Education (UE):</i> Generates basic knowledge of ES. Develops novel approaches or addresses fundamental research questions of societal importance. .....	Establishes relationships between ecosystem features and services. Identifies spatial priorities, often over large scales. Typically requires low ecological precision.	Presents a vision, develops strategies and objectives for achieving that vision, and tasks scientists with communicating to stakeholders the costs, benefits, and uncertainties of alternative actions. May perform scenario analysis. Requires intermediate level of ecological precision.	Implements specific actions, typically at small spatial scales. Precise biophysical information is valued at this phase.
	<i>Cost Benefit Analysis (CBA):</i> Utilizes valuation techniques to assess ES benefits in economic terms. .....			
	<i>Landscape Management (LM):</i> Informs on-the-ground ES management decisions.			

This selection process yielded 49 peer-reviewed publications that were subsequently reviewed in detail. We categorized each study according to two existing and complementary classification schemes. The first scheme used an ES decision framework that differentiates three contexts based on motivation: understanding and education, cost-benefit analysis, or landscape management (Fisher, Turner, & Morling, 2009). Because decisions on ES are often socially motivated, we consider studies that promote understanding and education to be relevant for decision making due to their potential influence on the perceptions, attitudes, and beliefs of stakeholders and decision makers who engage in decision processes (Ruckelshaus *et al.*, 2013). The second scheme described the scope of each study in relation to three operational phases: assessment, planning, or management (Knight, Cowling, & Campbell, 2006). We then merged these two categorizations to define the “decision context” that represents a study’s broader rationale and scope of inquiry (Table 2-1). These decision contexts are unique opportunities to ask policy questions, conduct analyses, engage with diverse decision-making audiences, and achieve distinct research goals (Maes *et al.*, 2012).

We reviewed each study and recorded information for the descriptive analysis. To satisfy stringent ES criteria and to avoid double counting of intermediate services (Ringold *et al.*, 2013), we classified hydrologic services based on their beneficial use (Brauman *et al.*, 2007). In recognizing the complexity of water resources management, we considered two classes of water supply benefits – those that are realized in-stream (*in situ*) and those that occur off-site (diverted *ex situ*).

Following other reviews, we considered five general categories of methods used to map and quantify ES: expert opinion, land cover proxy, empirical, conceptual water balance, and process-based (Seppelt *et al.*, 2011; Martinez-Harms & Balvanera, 2012; Crossman *et al.*, 2013).

Expert opinion is a subjective method in which scientists use their knowledge and experience to derive estimates. Proxy methods build on relationships between ecosystem characteristics and the provisioning of ES benefits and are used to assign ES values to different land cover types (Martinez-Harms & Balvanera, 2012). ES endpoints may also be estimated using empirical methods like Budyko curves for estimating long-term water balance (Zhang *et al.*, 2008) that use statistical techniques to fit quantitative relationships between predictor variables and a response variable. Whereas process models are physically-based and explicitly represent hydrologic processes (Sivapalan *et al.*, 2011), conceptual methods for estimating water balance compartmentalize the hydrologic cycle into distinct precipitation, runoff, evapotranspiration, and storage components (Aghakouchak & Habib, 2010). In cases where the quantification of an HES involved multiple methods, we designated the primary method as that which most directly contributed to the estimate.

We extended this review to document additional aspects of an analysis that are independent of the method used but critical for decision making - collectively referred to as the “approach”. To characterize how the information presented in each study pertains to the decision context, we documented analytical relevance using three established attributes: credibility, legitimacy, and saliency (Cash *et al.*, 2002). *Credibility* refers to the perceived quality of information, *legitimacy* describes transparency and comprehensibility, and *saliency* refers to the applicability of information to decision making (Liu *et al.*, 2008).

We evaluated these three attributes using criteria we identified from within the ES literature (Table 2-2). Credibility was evaluated against two standards of scientific rigor and a third criterion for ecological realism (i.e., spatial dynamics). HES benefits are modified by the way they flow through and interact with the landscape. For example, diversions and withdrawals

affect water supply benefits that are realized downstream. To assess the credibility with which studies represented these spatial dynamics, we tallied the number of source, sink, flow, and use processes that were included in the method (Bagstad *et al.*, 2013b). Values ranged between 1 and 4, with a score of 1 reserved for studies that accounted for source areas only. Studies that accounted for multiple processes were scored based on the number of processes represented (2 = source + one additional process, 3 = source + two additional processes, 4 = all processes). We evaluated legitimacy against two criteria – one that addressed analytical transparency based on methodological complexity and relative ease of interpretation and another regarding stakeholder involvement. We assessed methodological transparency as a function of complexity including data, resource, and time requirements (e.g. Martinez-Harms & Balvanera, 2012), classifying methods as either transparent (score = 1) or not (score = 0; Table 2-2). Saliency was evaluated through multiple features of ES studies whose importance is expected to vary based on context. Simple criteria were recorded as binary variables by assigning a value of 1 to indicate that a study fulfilled that criterion and 0 otherwise. We re-scaled credibility scores from 0 to 1 to be consistent with other metrics. Scores were then aggregated as means or proportions of studies within each decision context that became the metric for all comparisons.

Table 2-2. Criteria for evaluating the credibility, legitimacy, and saliency of case study approaches to map and quantify HES. Numeric scores are indicated in parentheses.

<i>Attribute</i> (Liu <i>et al.</i> 2008)	<i>Criteria</i> (reference)	<i>Categories</i>	<i>Description</i>
<b>Credibility</b>	<b>Model evaluation</b> (Seppelt <i>et al.</i> 2011)	Yes (1)	Accuracy assessed using independent data
		No (0)	Accuracy of method untested
	<b>Uncertainty assessment</b> (Seppelt <i>et al.</i> 2011)	Yes (1)	Uncertainty of method quantified
		No (0)	No uncertainty analysis
	<b>Flow complexity</b> (Bagstad <i>et al.</i> 2013b)	(1 – 4)	Methods account for source, sink, transport, and use dynamics of HES. 1= source only; +1 for each additional process represented.
	<b>Legitimacy</b>	<b>Transparency of method</b> (Martinez-Harms & Balvanera 2012)	Land cover proxy (1)
Expert opinion (1)			HES determined with expert knowledge
Empirical (0)			Relationships among biophysical data describe HES
Conceptual water balance (1)			Water yield and storage estimated by accounting for other components of the hydrologic cycle including precipitation and evapotranspiration.
Process (1)			Models simulate physical and ecological processes that contribute to HES
<b>Stakeholder involvement</b> (Seppelt <i>et al.</i> 2011)		Yes (1)	Participants contribute to the study design or implementation
		No (0)	No formal stakeholder participation
<b>Saliency</b>	<b>Scenario analysis</b> (McKenzie <i>et al.</i> 2012)	Yes (1)	HES provision compared under alternative scenarios
		No (0)	Scenarios not considered
	<b>Tradeoffs</b> (Seppelt <i>et al.</i> 2011)	Yes (1)	Study considered how provision of one HES affects another
		No (0)	HES evaluated in isolation
	<b>Reporting units</b> (Seppelt <i>et al.</i> 2011)	Biophysical (0;1)	Physical or biological measures of water quantity/quality, sediment, or nutrient endpoint
		Monetary (0;1)	Economic units
		Relative Ranking (0;1)	Qualitative descriptions (e.g. low, medium, high)

### 2.3. Results

Peer-reviewed HES research (2003-2013) occurred globally with hotspots in China (15), Spain (6), and the United States (4). The scale of investigation varied considerably in spatial extent from site (< 100 km<sup>2</sup>, 5), to local (100 to 1000 km<sup>2</sup>, 8), to regional (1000 to 100000 km<sup>2</sup>, 27), to national (7) and to global (2).

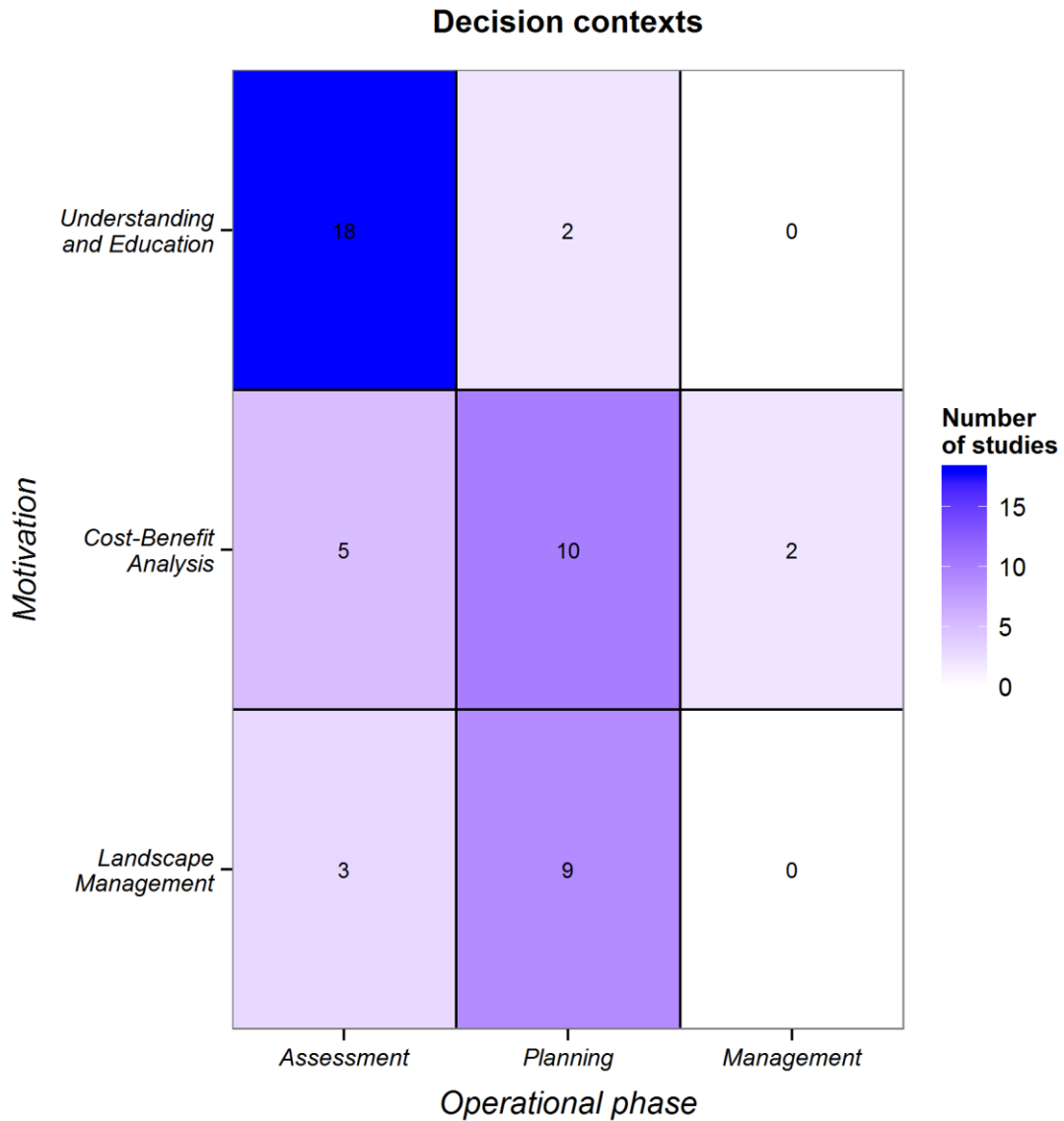


Figure 2-1. Characteristic contexts for decision making, with studies classified by motivation (Fisher *et al.* 2009) and operational phase (Knight *et al.* 2006). Counts reflect the number of studies in each decision context.



### 2.3.1 *What are the decision-making contexts represented in peer-reviewed HES research?*

We identified multiple drivers of HES research based on our classification of primary study motivation. Of the 49 case studies considered, motivations were fairly evenly distributed: 20 were classified as Understanding and Education, 17 evaluated ES benefits in the context of Cost-Benefit Analysis, and 12 were motivated by Landscape Management aims (Figure 2-1). The distribution of studies by operational phases was more skewed with the majority of studies addressing questions characteristic of the Assessment (26) and Planning phases (21), and only two studies associated with the Management phase.

HES related to diverted water supply benefits were most commonly assessed, accounting for 43% of all HES quantified, followed by water damage mitigation (40%), and *in situ* water supply (16%; Figure 2-2). Habitat supporting services accounted for 1% of quantified services, largely because most studies that focused on this supporting service did not state explicitly the service in terms of a benefit and were therefore rejected based upon our selection criteria. Of studies that investigated water damage mitigation services, 79% quantified sediment retention. Multiple HES were quantified in 22 studies, and of these studies, 12 assessed tradeoffs among HES.

### 2.3.2 *How do analytical approaches used to quantify HES benefits and changes in HES flows relate to quality of information, and how does this vary among decision contexts?*

Because some studies investigated multiple services, quantifying each with a different method, we present results for each effort to quantify a service. Of the five classes considered here (expert opinion, land cover proxy, empirical, conceptual and process-based; Table 2-2), empirical methods were utilized the most frequently (41). Process models (16), land cover proxy (14), and expert opinion (13) were similarly common. Conceptual methods were used less frequently (5). We also found associations between HES and the quantitative method used. For

example, sediment regulation was typically modeled (in 18 of 26 cases) using an empirical method (the Universal Soil Loss Equation; Crossman *et al.*, 2013) whereas hydrological process models were used almost exclusively (in 7 of 8 cases) to quantify water supply benefits.

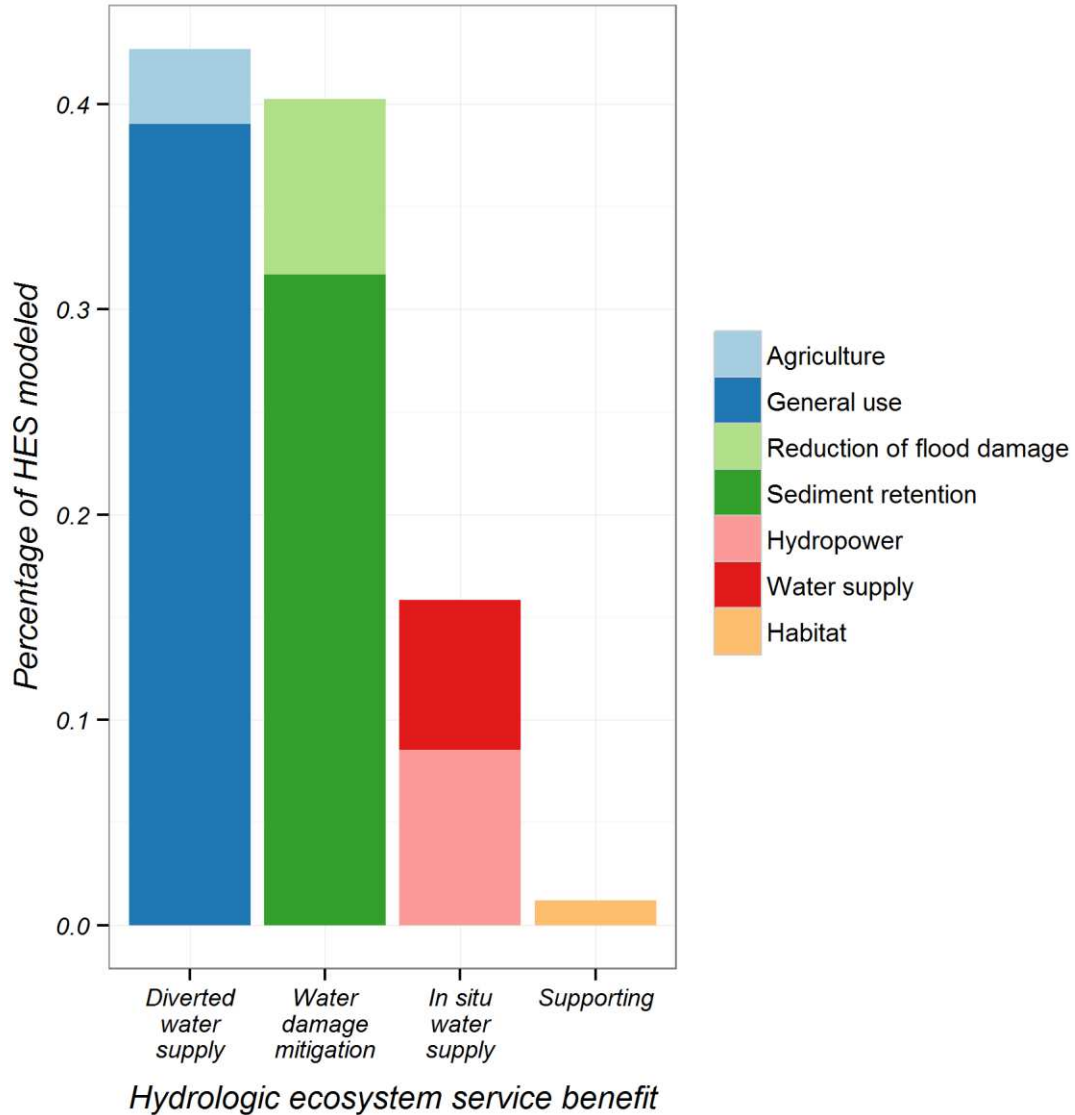


Figure 2-2. Percentage of hydrologic ecosystem services (HES) modeled, classified by benefit.

Approaches for quantifying HES differed in terms of credibility, legitimacy, and saliency when analyzed by case study motivation and scope of analysis (Figure 2-3). Mean credibility scores were highest for Understanding and Education (0.47) and Cost-Benefit Analysis (0.46)

and lowest for Landscape Management (0.38). Landscape Management, Understanding and Education, and Cost-Benefit Analysis ranked highest to lowest in terms of mean legitimacy scores but did not vary by a large margin (0.06). Attribute scores also varied by operational phase. For example, mean credibility scores were lowest for Assessment (0.33), moderate for Planning (0.48), and highest for Management (0.63).

Saliency criteria varied along two dimensions of the context (i.e., motivation and operational phase). Sliced by motivation, tradeoffs were most frequently assessed in Landscape Management (55%) and Understanding and Education (51%). By operational phase, tradeoffs were evaluated most frequently in the Planning phase (54%). Scenario analyses were most commonly conducted in the Management (100%) and Planning phase (92%). The highest flow complexity scores were observed in the Planning phase (mean = 0.51). The reporting of results in monetary units was most common among studies in the Cost-Benefit Analysis context, occurring in 70% of cases. Biophysical outputs and monetary outputs were reported in all three phases and motivations. Relative rankings were the least frequently used output.

## **2.4. Discussion**

The studies we reviewed quantified HES to answer basic research questions, evaluate different forms of watershed investment, and to inform management decisions. The vast majority of them (47) were exploratory in nature, focusing on baseline assessments and comparing alternatives in the planning phase, as opposed to prescribing specific treatments for management (2 studies).

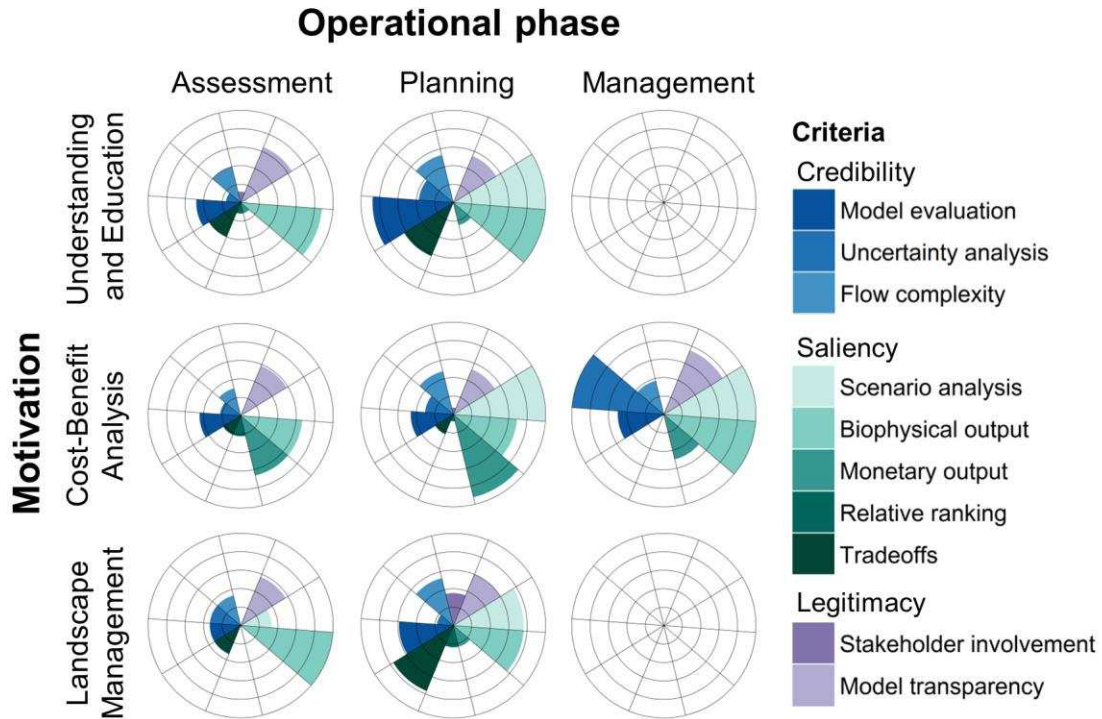


Figure 2-3. Approaches used to quantify hydrologic ecosystem services vary in terms of credibility (blues), legitimacy (purple), and saliency (green). These differences are visualized for distinct decision contexts with motivation classes organized by row and operational phases organized by column. We present results as the proportion of studies within each decision context that meet each criterion. In cases where a study analyzed multiple services, each effort to quantify a service served as the unit of analysis. The radial extent of each sector of the chart corresponds to this proportion and ranges between 0% and 100% (concentric circles represent 20% intervals).

#### 2.4.1 Approaches to quantify HES and their relevance to decision making

The approach to map and quantify HES varied in meaningful ways across decision contexts indicating that there are preferential strategies for investigating HES depending on research motivations and scope of analysis. When we evaluated methods and analyses in relation to the decision context of each study, three patterns emerged: 1) the most Credible approaches were typically encountered in advanced operational phases (i.e., Planning and Management); 2) Legitimacy scores were generally greatest in the Planning phase with stakeholder involvement occurring most frequently where Landscape Management is the motivation; and 3) Salient information varied with context but common ES analyses (e.g., tradeoff and scenario analyses) were conducted during the Planning phase.

Our findings align with previous research that suggests stakeholders are often incorporated into decision processes during the planning phase (Cowling *et al.*, 2008) when transparent, legitimate information is most critical (Cash *et al.*, 2002). Likewise, we found that scenario analyses and tradeoff evaluations were most commonly conducted in the Planning phase. Typical research questions addressed during this stage of analysis involve comparing alternatives, making scenario and tradeoff analyses highly salient in this context. We acknowledge that the studies included in this analysis represent a snapshot in time of the decision process that may proceed through assessment, planning, and management phases and that our results likely reflect information demands of stakeholders and decision makers involved at a particular phase. Suitable levels of credibility, legitimacy, and saliency may vary throughout the policy process in response to evolving priorities that can be driven by alternative objectives and level of stakeholder engagement (e.g., Cash *et al.*, 2002).

Interestingly, we found that HES benefits were associated with particular methods. Such associations are likely the legacy of distinct research traditions and may further explain apparent methodological disparities that exist among studies. In contrast to our findings, a recent review (Nahuelhual *et al.*, 2015) reported little correspondence between mapping purpose and methodological variables, but they considered all forms of ES rather than HES, which may account for some of the perceived difference.

We found that methods were rarely described in sufficient detail to permit independent replication. For example, methodological details, data sources and validation procedures were often incompletely reported. This finding supports the concerns of Seppelt *et al.* (2011) and highlights the need to ensure that peer-reviewed studies include all methodological information, in the manuscript or in supporting online information, to meet acceptable scientific standards for

transparency and replicability. Consistently reporting this information would advance the field in basic but essential ways that include providing an objective basis for evaluating the quality of research, as well as by setting objective benchmarks with which to compare studies and to establish best practices for ES research.

Ecosystem services are complex, arising when humans benefit from ecological processes (De Groot *et al.*, 2002). A critical feature of ES is the tradeoff that occurs when efforts to manage for one service diminish others (Rodriguez *et al.*, 2006). For example, a common tradeoff for water management occurs when decisions to capture diverted water supply benefits (e.g., irrigated agriculture) adversely affect in-stream benefits such as recreation and preservation of habitat (Auerbach *et al.*, 2014). Despite their potential value to decision making, tradeoff analyses were absent in roughly half of case studies that investigated multiple services.

As we have assessed here, study aims and scope are an appropriate lens for characterizing how relevant information varies across decision making contexts thereby influencing methodological considerations. However, we acknowledge that multiple factors shape how ES are quantified (Vigerstol & Aukema, 2011; Bagstad *et al.*, 2013; Crossman *et al.*, 2013). For example, Martinez-Harms & Balvanera (2012) suggested that the use of more robust methods is increasingly constrained by the availability of appropriate data. They conclude that the use of proxy methods and expert opinion is appropriate in data poor contexts and recommend that regression models be used in cases where primary data are available to produce the highest quality ES estimates. Without proper validation, however, it remains unclear how different methods compare in terms of reliability. To the extent that uncertainty and its acknowledgment influence the decision-making process, validation is likely to be an important step in understanding limitations of and establishing appropriate levels of confidence in modeled results

(Ruckelshaus *et al.*, 2013). Until models have thoroughly been validated, strategic monitoring offers a way to track outcomes (Brauman, 2015) and to test modeled results against observations.

Spatial mapping is a powerful tool for decision making and highly relevant and commonplace in ecosystem services research. Although we focused exclusively on studies that quantified HES using spatially-explicit methods for this reason, we recognize that non-spatial methods are also important for obtaining and communicating information at different stages of the policy process. For example, surveys that elicit willingness to pay can be used as part of a regional ecosystem services assessment to estimate the value placed on different services by a community.

Because our goal was to assess the state of peer-reviewed HES science, we did not consider grey literature or other sources in this review. Nonetheless, many of these studies are likely influential in informing decisions because they engage local experts and have local leadership (Ruckelshaus *et al.*, 2013). ES practitioners and decision makers may gain valuable insights from this body of knowledge.

#### 2.4.2 Knowledge Gaps

Using keywords, we initially selected 560 articles that self-identified as ecosystem services research. Of the articles that were not rejected based on title or abstract, approximately 10% (14 out of 135) were excluded for the primary reason that they were not expressed in terms of a benefit to people. As noted by Cowling *et al.* (2008) and substantiated by Seppelt *et al.* (2011), many ES assessments are not user-driven and are conducted irrespective of beneficiaries. To contribute to the consistency and substance of ES research, future HES studies should strive to clarify linkages between hydrological processes and benefits to humans. Although we were able to infer the primary motivation and operational phase of each study, details about connections to policy and management arenas were often lacking. For example, many case

studies mentioned the relevance of their work for decision making but did not explicitly comment on the decision processes or actors that would be involved. To facilitate future discourse and integration into decision making, authors should discuss contexts where their analyses are most appropriate and likely to be informative. Scientists aiming to produce decision-relevant science will benefit from understanding links between their research and policy and management outcomes. Tailoring research to decision contexts using approaches that maintain desired levels of credibility, legitimacy, and saliency can increase the likelihood of achieving these aims (Game, Schwartz, & Knight, 2015).

The interplay between science and decision making may be characterized by an analogy that describes the process in terms of a supply of and demand for scientific information. Sarewitz & Pielke (2007) consider scientists to be the suppliers of knowledge and information while demand is driven by actors who incorporate this information into their decision making, and argue that improved societal outcomes can be achieved by reconciling supply and demand. In conducting this review, we used three essential attributes of useful information to characterize how scientific information has been supplied in various contexts. To judge the usefulness in practice of different approaches, future research may investigate the demand-side of the science-decision making process by focusing on the information needs and preferences of decision makers.

Despite the value of habitat supporting services (De Groot *et al.*, 2012), the benefits of these services were quantified in only one study. More research is needed to uncover the role of supporting services in the production of other services to strengthen economic accounting (Boyd & Krupnick, 2009) and to inform ES management (Brauman *et al.*, 2007).



Quantifying ES requires sophisticated conceptualization and simplification of complex social and ecological processes. Flows of HES follow preferential pathways across the landscape according to topography and human infrastructure, making them amenable to tracking. This is a significant feature of HES because water quality and quantity and thus potential benefits vary in space and time. Despite having the ability to track these changes, we found that most case studies did not account for spatial dynamics, an oversimplification that could greatly bias estimates of HES benefits (e.g., overestimation of *in situ* benefits that results from neglecting upstream water diversions). Indeed, this simplification can lead to incorrect views that HES benefits are evenly distributed among different groups when in reality there may be clear differences expressed in terms of geography and/or segments of the population (Mandle *et al.*, 2015). In the future, continued development of methods to simulate the flow and modification of HES from *source to use* locations (Bagstad *et al.*, 2013b) on the landscape will greatly improve our understanding and management of these services.

## **2.5. Conclusion**

Globally, decision makers increasingly make use of HES concepts and tools to address freshwater management issues (Guswa *et al.*, 2014). Our aims in this paper were to firstly document the context for these decisions and secondly to understand how research methods align with key study dimensions. We found compelling evidence that much of the variability in the quantification of HES can be explained by research motivations and scoping, reflecting the decision-oriented framing of the ES concept. We also found associations between HES and particular methods, likely legacies of distinct research traditions. We detected generally low levels of validation. We also identified key knowledge gaps in the state of the science including the need to differentiate ES assessments from biophysical assessments (i.e., to clarify linkages

between hydrological processes and benefits to humans) as well as to clearly articulate target audiences and decision contexts.

The framing and contextualization we employed in our analysis (Table 2-1) offers several key advantages. Decision makers can review studies conducted in similar contexts to learn how past approaches were used to inform those decisions. This information may be used to evaluate how standards for scientific research vary throughout stages of the policy process (e.g. assessment, planning, and management phases). Framing studies within such a classification can aid researchers, practitioners, and decision makers in identifying goals, formulating relevant questions, and selecting informative approaches for quantifying HES. Likewise, a structured inquiry into the aims and scope of a given decision context can assist ES researchers in providing contextualized information most likely to be used by decision makers. Ultimately, research efforts that strive to link science with policy processes by providing robust, meaningful, and interpretable information may have the greatest impact on decision making (Rosenthal *et al.*, 2015).

To advance HES science, we offer to researchers the following suggestions to strengthen their contributions to the field of ES and their utility for decision makers. For each suggestion, we additionally highlight salient case studies from our review that exemplify each of these practices.

Increase publication of management-oriented studies - advance the types of knowledge needed to inform on the ground decision making in peer-reviewed as well as grey literature outlets. Having a robust scientific basis to guide local land use decisions can ultimately provide significant ecosystem service benefits because these decisions often take place in contexts that are supported by established decision pathways and strong stakeholder engagement (Cowling *et*

*al.*, 2008). For example, Arias *et al.* (2011) developed an analytical framework to assess the costs and benefits of forest conservation for a proposed hydropower operation. They demonstrate how this information could be incorporated into the design for a payment for ecosystem services scheme in this particular management context but also describe how successful implementation of their framework to other proposed projects would require incorporating local knowledge as well as input from beneficiaries and watershed managers.

Identify beneficiaries – Explicitly identify the parties and geographies that benefit from each service. This will serve the dual purpose of clarifying relevant ES and will facilitate efforts to engage stakeholders. Disaggregating benefits among different groups will also increase the policy-relevance and uptake of studies that serve heterogeneous populations. Locatelli *et al.* (2011) identified hydroelectric companies as beneficiaries and differentiated between two types of users each with characteristic needs, objectives and management considerations. To quantify the benefits that would ultimately be received by each user type under different watershed management scenarios, they tracked the flow of ecosystem services from source to use areas accounting for hydrologic features (i.e. dams, lakes and water intakes) that would influence the benefits realized downstream.

Provide context - Describe the study's motivations, scope of work, and explicit linkages to decision processes. Confer with stakeholders and decision makers to evaluate preferred attributes (i.e., credibility, legitimacy, saliency), research questions, and relevant scenarios. Indicate why particular methods were preferred (e.g., data requirements, technical expertise, ease of interpretation). Notter *et al.* (2012) enumerated several important criteria for their study including the need to a) consider water supply requirements communicated by stakeholders b) provide results at scales amenable to decision making and c) to maintain transparency by

communicating uncertainty of their research. By adhering to these criteria they conclude that their indicators “are appropriate for use in decision-making processes involving stakeholders”.

Document methods, assumptions, and uncertainties transparently – Describe methods and data sources in sufficient detail to enable independent replication of analysis, and include information on parameterization, scale and transferability to other geographies. List key assumptions relating to the validity of the analysis, and provide accuracy assessments to inform decision makers with notable uncertainties. This practice is well demonstrated by Immerzeel, Stoorvogel, & Antle (2008) who validated their hydrologic model and produced plausible range estimates for the results of their economic model using a sensitivity analysis. In addition, they listed a number of key assumptions behind their modeling approach along with their implications.

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### **3 Characterizing anthropogenic and natural drivers of the occurrence of cold-water and cool-water fishes in the western United States**

#### **3.1. Introduction**

Globally, environmental changes are occurring in ways that are profoundly important for freshwater ecosystems with consequences for the occurrence of species (Revenga *et al.*, 2005; Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010). Understanding the distribution of species in relation to the environment is a long-standing goal of ecology that has become more urgent in recent decades due to rapid global change (Guisan & Thuiller, 2005). Traditionally, ecologists have investigated the distribution of freshwater species using environmental correlates at multiple spatial scales, e.g. (Vannote *et al.*, 1980; Minshall *et al.*, 1985; Tonn, 1990; Schlosser, 1991) and have largely focused on the effects of natural sources of variability including climate, habitat and resource availability (Frissell *et al.*, 1986; Matthews, 1998; Jackson, Peres-Neto & Olden, 2001).

One approach for characterizing natural environmental drivers of species distributions has been to focus on reference sites thought to be minimally influenced by human activities (Stoddard *et al.*, 2006; Pont *et al.*, 2009; Poff *et al.*, 2010). Reference sites are viewed as a way to distinguish between natural and anthropogenic influences on biological condition (Hughes *et al.*, 1998; Hawkins *et al.*, 2000; Pont *et al.*, 2006). The reference approach is well suited for establishing biological expectations that serve as benchmarks of ecological condition but has limited application to understanding contemporary drivers of species distribution for two primary reasons. First, human influences on streams are pervasive (Poff, Bledsoe & Cuhaciyan, 2006; Allan & Castillo, 2007), making it likely that observed biological metrics reflect anthropogenic effects (Whittier *et al.*, 2007; Pont *et al.*, 2009), but these are not explicitly accounted for in

reference-based assessments. This weakens ecological inferences on expected condition and limits understanding of environmental drivers. Second, reference sites have few analogs in contemporary landscapes, thereby limiting the geographic scope and transferability of insights obtained from species distribution models. For example, in a recent survey of flowing waters in the United States, only 28% of the nation's stream miles were found to be in "good" biological condition compared to reference sites (EPA, 2016). With rivers and streams embodying a wide range of conditions (Esselman *et al.*, 2011), adequately characterizing modern day drivers of species occurrence requires assessing watersheds across natural and disturbed gradients (Clapcott *et al.*, 2012; Domisch *et al.*, 2015).

In recent decades, growing concerns over climate change have further contributed to the need to assess changes to climatic and environmental drivers of species occurrence. Climatic variables can no longer be considered stationary (Milly *et al.*, 2008), therefore modeling efforts must shift their focus to dimensions of climatic variability whose changes are likely to be most consequential from an ecological standpoint (Garcia *et al.*, 2014). Despite this urgency, predicting ecological responses to climate change remains a key conservation challenge (Olden *et al.*, 2010) with difficulties posed by nonlinearities (Pilière *et al.*, 2014) and interactions among multiple drivers that include human pressures (Townsend, Uhlmann & Matthaei, 2008; Nelson *et al.*, 2009a; Palmer *et al.*, 2009; Kuemmerlen *et al.*, 2015). Capturing the form of response is critical for identifying thresholds along environmental gradients (Karr, 1999) that can be used to inform environmental assessments and to establish standards for management. As evidence continues to mount of the diverse ways in which human activities influence flowing waters (Graf, 1999; Allan, 2004; Palmer *et al.*, 2008; Vorosmarty *et al.*, 2010), modeling efforts that can disentangle the role of environmental drivers (Pilière *et al.*, 2014) and project changes in species'

distributions as a result of human activities are becoming increasingly relevant to management and conservation issues (Steen, Wiley & Schaeffer, 2010).

The aim of this study was to investigate the drivers of western US cold- and cool-water riverine fish species occurrence within the context of global change. We focused on cold and cool thermal guilds as those species are presumed to face the greatest risk to increasing temperatures in the western US that have been implicated by regional climate projections (Walsh *et al.*, 2014). Specifically, we examined the following research questions: (1) What are the natural and anthropogenic drivers that influence the occurrence of cold- and cool-water fish species and what is the relative contribution of various anthropogenic drivers in shaping fish species occurrence? (2) How do species-environment relationships vary across broad environmental gradients that exist within historic native ranges? and (3) What drivers of species occurrence interact most strongly?

To investigate our questions, we developed species distribution models (SDMs) using field-based and remotely sensed data to predict the occurrence of cold- and cool-water fishes across the western US. Following Allan (2004), we sought to establish mechanistic linkages between human activities and stream conditions that would directly influence fish occurrence, in order to support ecological interpretation of human influence. Thus, our model incorporated anthropogenic predictors that characterize the range of stream conditions existing across our study area. In addition, we evaluated the response of species across broad natural and anthropogenic environmental gradients that exist within their historic native ranges and assessed interactions among predictors.

Our full-gradient, mechanistic approach provides new insight that is broadly applicable across gradients of human disturbance characteristic of modern stream landscapes. We also

discuss the significance of capturing broad natural environmental gradients to characterize species' environmental niches, using thermal niches as an example. By focusing on thermally-sensitive species, we provide a basis for gaining insight into how environmental drivers that shape the occurrence of those species in the region will interact with climate warming to affect future shifts in species distributions.

## **3.2. Methods**

### *3.2.1 Stream survey data*

We compiled biological, chemical, and physical data collected as part of a regional stream assessment. Between 2000 and 2004, the US Environmental Protection Agency's Environmental Monitoring and Assessment Program (WEMAP) Western Pilot surveyed a total of 1,368 probabilistic and hand-picked sites on perennial streams and rivers covering the 12 western states. Survey sites were stratified by state using an unequal-probability, spatially-balanced design (Stevens & Olsen, 2004) that selected 120 sites for each of four Strahler-stream order classes (first, second, third, fourth and higher order streams), plus 120 sites for large rivers. The same sampling design was used to select additional sites for intensive study areas in California, Oregon, Washington, Colorado, and North and South Dakota. Aquatic vertebrate sampling was conducted using backpack electrofishing in first- to third-order streams and via raft electrofishing in fourth-order and larger rivers (Whittier *et al.*, 2007). To augment fish occurrence records, we pooled data from the National Rivers and Streams Assessment (NRSA), a national level assessment conducted by the US Environmental Protection Agency that randomly surveyed 1,924 sites representing perennial rivers from 2008-2009. Fish count data were converted to presence/absence (Leathwick *et al.*, 2005). We excluded sites with incomplete fish, physical, and chemical records and retained only those sites that were considered

independent (i.e. not repeat surveys). In total, data collected at 765 sites covering 10 states were used in our analysis.

### 3.2.2 Species selection criteria

We used a fish trait database (Mims *et al.*, 2010; Mims & Olden, 2013; Olden, Unpublished data) to identify fish species possessing cold- or cool-water trait states. From this list of candidate species, we selected focal species that were: (1) classified as cold- or cool-water species that primarily inhabit flowing waters; (2) observed at a minimum of 20 sites for which we had stream temperature data; and (3) were non-anadromous. We retained only those fish observations collected within species’ historic native ranges. Historic range maps were obtained from NatureServe (2010) and were delineated at the scale of fourth-level watersheds (i.e. HUC 8) according to taxonomic records and expert opinion. Six species from four families met these criteria (Table 3-1). Species’ occurrences are shown in Figure 3-1.

Table 3-1. Native cold- and cool-water species included in this analysis. Sites refer to survey locations within species’ historic native ranges.

<b>Common name</b>	<b>Family</b>	<b>Genus and species</b>	<b>Sites present</b>	<b>Sites absent</b>
Mountain sucker	Catostomidae	<i>Catostomus platyrhynchus</i>	32	150
Mottled sculpin	Cottidae	<i>Cottus bairdii</i>	38	124
Longnose dace	Cyprinidae	<i>Rhinichthys cataractae</i>	26	213
Speckled dace	Cyprinidae	<i>Rhinichthys osculus</i>	51	242
Cutthroat trout	Salmonidae	<i>Oncorhynchus clarkii</i>	91	265
Rainbow trout	Salmonidae	<i>Oncorhynchus mykiss</i>	190	110

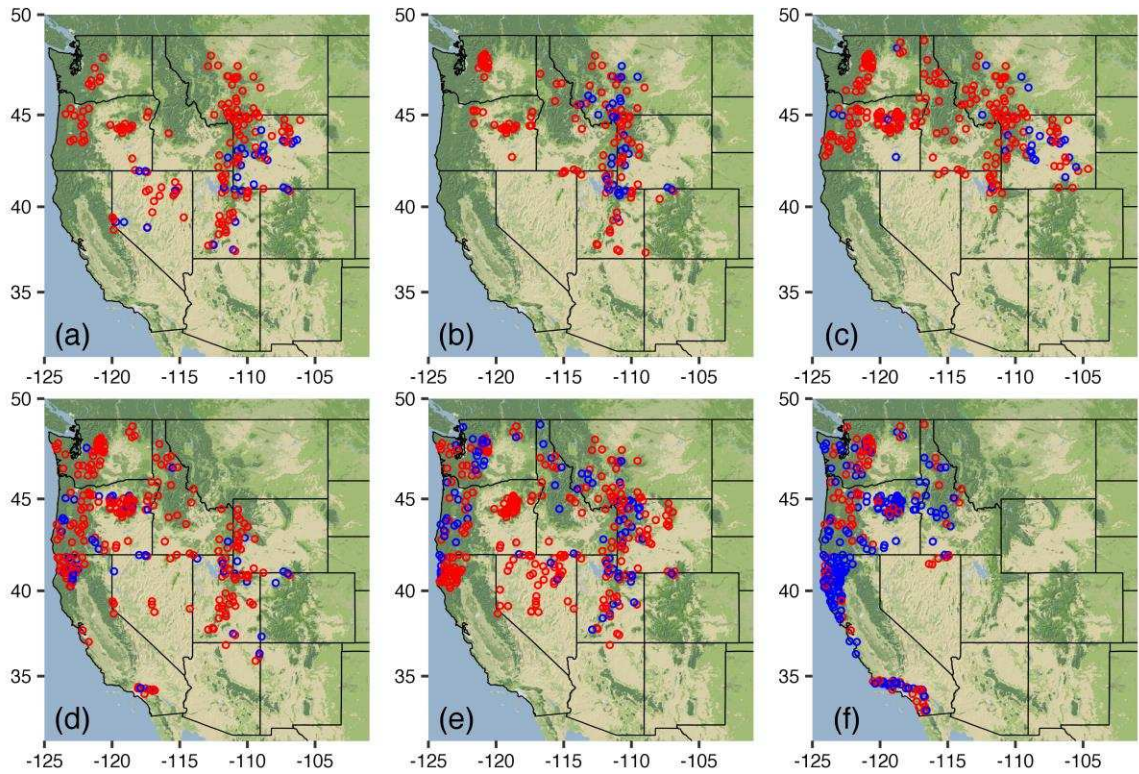


Figure 3-1. The 765 sites from WEMAP and NRSA surveys of flowing waters in the western United States that were included in this analysis, grouped by historic native geographic range of six cold- and cool-water fish species: a) mountain sucker, b) mottled sculpin, c) longnose dace, d) speckled dace, e) cutthroat trout, and f) rainbow trout. Red symbols indicate absence, blue symbols indicate presence.

### 3.2.3 Environmental data

We compiled several habitat measurements collected for the WEMAP and NRSA surveys for use as site and reach-scale predictors of fish distribution. From an array of candidate environmental variables, we selected a parsimonious set of field-based measurements representing substrate type, embeddedness, riparian cover, and valley confinement (Kaufmann *et al.*, 1999; Peck *et al.*, 2006). We complemented these field-based measures of stream habitat with a suite of GIS-based catchment scale variables (described below) to serve as predictors for our species distribution models (Table 3-2). Linkages between fish assemblages and these environmental variables have previously been established and are described concisely here (for further detail, see Table A1 - 1). Briefly, substrate size distribution is important for spawning habitat and oxygenation of eggs (Poff, 1997; Webb *et al.*, 2008). Embeddedness is a measure of

the accumulation of fine sediments within substrate that has physiological and reproductive relevance to fishes (Kemp *et al.*, 2011). Riparian zones are the interface between terrestrial and freshwater environments, with streamside vegetation providing diverse and critical stream habitat functions (Gregory *et al.*, 1991; Naiman & Decamps, 1997). Valley confinement sets the geomorphic context for stream habitat with implications for floodplain interactions, groundwater upwelling associated with hyporheic exchange and the cooling/oxygenation of water, and moderation of high flows that can scour eggs from nests (Baxter & Hauer, 2000; Poole & Berman, 2001).

Streamflow has been described as a master variable (Power *et al.*, 1995) with influence over critical ecological characteristics of river systems that include water quality, stream temperature, substrate, and habitat features (Poff *et al.*, 1997; Xenopoulos & Lodge, 2006). We obtained estimates of mean annual flow from the NHDPlusv2 dataset (<http://www.epa.gov/waterdata/nhdplus-national-hydrography-dataset-plus>) and scaled them by drainage area to derive mean annual flow (MAR), an indicator of relative stream size and streamflow permanence (Pyne & Poff, 2016).

Vertebrate sampling for WEMAP and NRSA occurred primarily during summer (June - August), when species are most likely to experience thermal constraints during peak stream temperature (Roberts *et al.*, 2013). We obtained August mean stream temperature estimates representing a 19-year historical baseline (1993-2011) from NorWeST, a regional spatial statistical network model validated against an extensive database of stream temperature records ([www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html](http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html)). Spatial statistical models account for longitudinal and flow-related spatial dependence that occur on stream networks (Ver Hoef, Peterson & Theobald, 2006; Isaak *et al.*, 2014). Isaak *et al.* (2015) provides a recent application

of the NorWeST data to fish distribution modeling. We focused on maximum stream temperature as opposed to air temperature for its direct role in shaping the distribution of cold- and cool-water fish species. In addition, because modeled general circulation model (GCM) projections for our study area tend to converge on the magnitude and directionality of temperature change (Walsh *et al.*, 2014), we focused on a climate driver whose importance is likely to increase into the future, regardless of land use changes.

### *3.2.4 Catchment-scale anthropogenic variables*

To account for the multiple influences of land use on stream ecosystems, we followed Allan's (2004) framework and incorporated several anthropogenic variables, each targeting a particular constraint imposed by human activities on freshwater ecosystems (Table 3-2). We hypothesized that use of ecologically relevant metrics would advance a mechanistic understanding of the pathways by which human activities influence fish occurrence in ways that would not be possible using traditional landscape metrics (e.g. proportion of watershed in a given land use). We represented the effects of broad-scale land use on stream condition by deriving cumulative estimates of sedimentation, nutrient enrichment, and contaminant pollution produced within the upstream catchment. We modeled sedimentation as a function of urban and agricultural land use, catchment slope, soil erodibility, and rainfall-runoff erosivity. To account for nutrient influences on water quality, we developed a spatial allocation model to map county-level estimates of nitrogen and phosphorus inputs (Ruddy, Lorenz & Mueller, 2006) into their constituent sources (e.g. agricultural practices, atmospheric nitrogen deposition) at fine (270 m) spatial resolution. We represented broad-scale contaminant pollution using the presence of National Pollutant Discharge Elimination System (NPDES) sites and the areal extent of mineral operations (Soulard *et al.*, 2016). We applied a weighting scheme to catchment-scale predictors (see ) to account for spatial variability in the potential for an upland area to influence



downstream conditions by integrating local measures of proximity to the stream network and level of hydrologic activity (Peterson *et al.*, 2011). For each land use disturbance variable  $j$ , we computed the cumulative disturbance (CD) in a catchment as:

$$CD_j = \sum W_i F_i D_{ij}$$

where  $W_i$  is a 0-1 weighting factor that represents the inverse flow length from the cell  $i$  to the outlet,  $F_i$  is flow accumulation in cells at cell  $i$ , and  $D_i$  is the amount of disturbance at cell  $i$ . Cumulative disturbance measures were normalized by drainage area to account for variation in catchment size (Esselman *et al.*, 2011).

We produced two catchment-scale indicators to estimate the level of hydrologic alteration. Our index of flow modification was calculated as a ratio value comparing the cumulative upstream storage volume to the virgin mean annual discharge (Graf, 1999; Nilsson *et al.*, 2005). Flow modification values generally range from 0-1 with values of zero indicating unmodified flow and higher values indicating increased reservoir storage. We computed cumulative upstream storage as the sum of normal reservoir storage for all upstream facilities contained within the National Inventory of Dams (USACE, 2015). Mean annual flow rates estimated from reference gauges using the Enhanced Runoff Method (EROM) (Falcone, Carlisle & Weber, 2010; McKay *et al.*, 2012) were obtained from the NHDPlusv2 dataset. EROM flow rates, which were estimated using regression equations calibrated to sites with minimal anthropogenic influence, were converted to volumetric units and served as our measure of virgin mean annual discharge. We also quantified the extent of agriculturally-related hydrologic infrastructure using an index to represent the proportion of the length of all stream reaches coded as artificial canals, pipelines or ditches in the NHDPlusv2 dataset to the total length of stream

reaches within each catchment. Spatial analyses were performed in ArcGIS 10 (ESRI, Redlands, CA, USA) and Google Earth Engine.

### *3.2.5 Species Distribution Models*

We modeled the probability of occurrence for each species as a logistic function using Boosted Regression Trees (BRTs). BRTs are a powerful method of machine learning that are well-suited for non-linear data, do not assume distributions, are robust to collinearity issues, and effectively account for interactions due to the hierarchical nature of trees. In addition to these advantages, the predictive ability of BRTs has been shown to be greater than competing statistical methods including Generalized Linear Models (GLM) and Generalized Additive Models (Guisan *et al.*, 2007; Elith, Leathwick & Hastie, 2008), particularly when confronted with complex, non-linear responses. Unlike single regression trees (e.g. Classification and Regression Trees), BRTs consist of a sequence of trees built on repeatedly modified versions of the data for which increased weights are applied to observations that were poorly predicted at the previous stage (i.e. boosting). Observations that are difficult to classify become more influential at each iteration (Hastie, Tibshirani & Friedman, 2009). Existing trees do not change at each stage and the final BRT model is a linear combination of many trees (Elith, Leathwick & Hastie, 2008). BRTs have previously been used in freshwater ecology research (for recent examples see Clapcott *et al.*, 2012; Pilière *et al.*, 2014; Leathwick *et al.*, 2016).

Table 3-2. Description of natural environmental predictors of cold-water and cool-water fish occurrence and underlying anthropogenic disturbance gradients in the western United States. Anthropogenic influences were quantified according to hypothesized disturbance mechanisms (Allan, 2004). Anthropogenic predictors are associated with disturbance mechanisms as follows: *DSED* = sedimentation, *DNE* = nutrient enrichment, *DCP* = contaminant pollution, *DHA* = hydrologic alteration.

<b>Variable name</b>	<b>Description</b>	<b>Mean and range</b>
<i>RchSlope</i>	Mean reach slope (%)	4.6, 0 - 36
<i>RchSubstrate</i>	Proportion of reach composed of sand and fine RchSubstrate (%)	24.5, 0 - 100
<i>RchRiparian</i>	Woody riparian cover within reach (sum of ground, mid and canopy layers; areal proportion)	0.8, 0 - 2.8
<i>RchConfine</i>	Channel confinement (ratio of stream length to valley width; unitless)	1.2, 1 - 10.4
<i>RchStreamT</i>	Mean August stream temperature of reach (°C)	13.7, 3.8 - 26.1
<i>CatBaseflow</i>	Baseflow as proportion of total flow within catchment (%)	59.9, 14.2 - 85
<i>CatMAR</i>	Mean Annual Runoff (m <sup>3</sup> /s/km <sup>2</sup> ): Mean Annual Flow (m <sup>3</sup> /s) / Upstream drainage area (km <sup>2</sup> )	0.03, 1.4 x 10 <sup>-7</sup> - 0.6
<i>RchDSED_Embed</i>	Fraction of particle's surface surrounded by fine sediments (%)	49.3, 2 - 100
<i>CatDHA_FlowMod</i>	Hydrologic alteration quantified as proportion of virgin mean annual yield stored behind dams within catchment (fraction)	0.2, 0 - 10
<i>CatDHA_Canals</i>	Hydrologic alteration quantified as length of canals, ditches, and pipelines / length of streams within catchment (fraction)	0.01, 0 - 0.5
<i>CatDSED_Sed</i>	Cumulative erosion within catchment (tons/year/km <sup>2</sup> , HW)	6.8 x 10 <sup>5</sup> , 0 - 3.9 x 10 <sup>7</sup>
<i>CatDNE_N</i>	Cumulative nitrogen inputs within catchment (kg/year/km <sup>2</sup> , HW)	1.9 x 10 <sup>5</sup> , 1.1 x 10 <sup>2</sup> - 4.9 x 10 <sup>6</sup>
<i>CatDNE_P</i>	Cumulative phosphorus inputs catchment (kg/year/km <sup>2</sup> , HW)	1.2 x 10 <sup>4</sup> , 0 - 1.2 x 10 <sup>6</sup>
<i>CatDCP_Mines</i>	Surface area of mines / catchment area (% , HW)	9.4 x 10 <sup>-7</sup> , 0 - 3.2 x 10 <sup>-4</sup>
<i>CatDCP_Discharge</i>	Permitted discharge locations (# sites/km <sup>2</sup> , HW)	1.3 x 10 <sup>-3</sup> , 0 - 0.9

See Supplemental Information for detailed explanation of predictors including use of a hydrologic weighting (HW) scheme to account for spatial variability in land use influence.

Following guidance from the BRT literature (Elith, Leathwick & Hastie, 2008; Hastie, Tibshirani & Friedman, 2009), we fit models with varying values for tree depth (1-4) and learning rate (0.0005, 0.001, 0.005, 0.01). We selected a maximum tree depth of four as a compromise between model complexity and interpretability (following Clapcott *et al.*, 2012; Pilière *et al.*, 2014). Tree depths greater than one are not forced into the BRT model and are only fit when supported by the data. For all models, we set a maximum number of trees to 6,000 and used a bagged fraction of 0.6 (Elith, Leathwick & Hastie, 2008).

Models were trained using 10-fold cross validation repeated five times to improve the stability of estimates (Kohavi, 1995; Leathwick *et al.*, 2006). We evaluated the performance of each candidate model (a function of learning rate, tree depth, and number of trees) on withheld subsets of the data and determined optimal model complexity as that which maximized the area under the curve statistic (AUC) and contained a minimum of 1,000 trees (Elith, Leathwick & Hastie, 2008). AUC values greater than 0.7 generally indicate good discrimination between presence and absence; values greater than 0.9 reflect excellent discrimination by a model (Pearce & Ferrier, 2000).

BRT models can be interpreted via several mechanisms. For example, we evaluated the strength of association between species occurrence and the suite of predictor variables using a measure of relative importance (Hastie, Tibshirani & Friedman, 2009). Relative importance accounts for the number of times a predictor is involved in splitting a tree, weighted by the sum of improvements in squared error due to all splits involving that predictor, and averaged over all trees. The relative importance of predictors is scaled to sum to 100% for each model, with higher values indicating greater influence on the response (Elith, Leathwick & Hastie, 2008). Partial dependence plots were produced to illustrate the dependence of species occurrence on individual

predictors across a gradient of values, conditional on all other predictors (Friedman, 2001). The form of response indicates how the relative probability of occurrence changes along environmental gradients (Bond *et al.*, 2011). We assessed the strength of interaction for all pairwise sets of predictors in our final model using Friedman’s H statistic (Leathwick *et al.*, 2006; Friedman & Popescu, 2008). H ranges between 0 and 1 with higher values corresponding to stronger interaction effects. All analyses were performed using R version 3.2.2. BRT models were fit using the gbm package version 2.1.1. The caret package version 6.0-52 was used to tune the model parameters.

### 3.3. Results

#### 3.3.1 Performance of species distribution models

Distribution models for cold- and cool-water fish species using natural and anthropogenic environmental predictors performed adequately, with cross-validated AUC values ranging from 0.69 to 0.91 (mean = 0.828 ±0.05; Table 3-3). We obtained correct classification rates (CCR) of 66% - 84% using species prevalence as the probability threshold. With the exception of longnose dace for which zero interactions were modeled, tree depths for the best fitting species models ranged between three (mountain sucker, speckled dace) and four (mottled sculpin, cutthroat trout, rainbow trout).

Table 3-3. Summary of fish species distribution models built using boosted regression trees. Estimates of model performance that include area under the receiver operating characteristic curve (AUC) and correct classification rate (CCR) were obtained using cross-validation procedures.

<b>Species</b>	<b>Number of trees</b>	<b>Tree depth</b>	<b>Learning rate</b>	<b>AUC</b>	<b>CCR</b>
Mountain sucker	3200	3	0.0005	0.83	76%
Mottled sculpin	6000	4	0.001	0.78	73%
Longnose dace	7550	1	0.001	0.91	84%
Speckled dace	3100	3	0.0005	0.88	80%
Cutthroat trout	1250	4	0.005	0.69	66%
Rainbow trout	6350	4	0.0005	0.80	70%

### 3.3.2 Influence of natural and anthropogenic environmental drivers on occurrence of cold- and cool-water fish species

Species distribution models were primarily driven by a subset of key predictors found to be influential for a majority of species. Top predictors included natural environmental variables describing hydrogeomorphic and climatic gradients and anthropogenic environmental variables relating to various aspects of stream condition. For each species, we report the five most influential predictors, presenting predictors in order of their mean relative influence across all species (Table 3-4). Reach slope (*RchSlope*) contributed 17% to model outcomes on average and was among the top five predictors for all species except cutthroat trout. Cumulative nitrogen (*CATDNE\_N*) ranked among the top five predictors for all six fish species and accounted for 17% of model outcomes, on average. Stream temperature (*RchStreamT*) contributed 15% to model outcomes on average, ranking among the top five predictors for all five cold-water fish species; it was the least influential for mountain sucker, the only cool-water species. Among hydrologic variables, mean annual runoff (*CatMAR*) was the most influential predictor for cutthroat trout (18%), second most influential for mottled sculpin (10.9%), ranked fourth for mountain sucker (7.5%) and contributed 8% to model outcomes on average across all species. Baseflow was a top five predictor for mountain sucker and cutthroat trout and contributed 7% on average across all species. Flow modification was among the most influential predictors for both cyprinid species, ranking fourth for speckled dace and fifth for longnose dace. Embeddedness, a measure of substrate impairment, ranked among the top five predictors for both salmonid species cutthroat trout and rainbow trout, as well as for mottled sculpin and speckled dace, and accounted for 6% of model outcomes on average.

Table 3-4. Five most influential predictors relating the occurrence of five cold-water and one cool-water fish species to the environment. Relative importance of predictors is indicated in parentheses and reflects the percent contribution (out of 100%) of a predictor to a species model. Anthropogenic predictors are associated with disturbance mechanisms as follows: *DSED* = sedimentation, *DNE* = nutrient enrichment, *DCP* = contaminant pollution, *DHA* = hydrologic alteration. Note that *Cat* and *Rch* labels are excluded here. See Table 3-2 for full predictor abbreviations.

<b>Mountain Sucker</b>	<b>Mottled Sculpin</b>	<b>Longnose Dace</b>	<b>Speckled Dace</b>	<b>Cutthroat Trout</b>	<b>Rainbow Trout</b>
<i>Slope</i> (28.4)	<i>Slope</i> (18.7)	<i>DNE_N</i> (22.4)	<i>StreamT</i> (34.8)	<i>MAR</i> (18)	<i>StreamT</i> (21.6)
<i>DNE_N</i> (18.3)	<i>MAR</i> (10.9)	<i>DHA_Canals</i> (22.3)	<i>DNE_N</i> (19.9)	<i>Baseflow</i> (12.2)	<i>DNE_N</i> (17.7)
<i>Baseflow</i> (14.7)	<i>DNE_N</i> (10.6)	<i>Slope</i> (21.1)	<i>Slope</i> (15.2)	<i>DNE_N</i> (12.1)	<i>Slope</i> (13.1)
<i>MAR</i> (7.5)	<i>DSED_Embed</i> (8.7)	<i>StreamT</i> (12.2)	<i>DHA_FlowMod</i> (6.1)	<i>DSED_Embed</i> (10.5)	<i>Substrate</i> (12.1)
<i>Confine</i> (5.6)	<i>StreamT</i> (8.4)	<i>DHA_FlowMod</i> (9.9)	<i>DSED_Embed</i> (4.9)	<i>StreamT</i> (10.4)	<i>DSED_Embed</i> (8.7)

### 3.3.3 Contribution of disturbance mechanisms

Anthropogenic influences contributed substantially to all species models, with total contributions (i.e. sum of relative influences) ranging between 61.3% for longnose dace and 32.6% for cutthroat trout. Grouping anthropogenic predictors by their associated disturbance mechanism (Allan, 2004) revealed that factors with the greatest mean influence on species occurrence related to nutrient enrichment followed by sedimentation and hydrologic alteration (Figure 3-2). Of the four disturbance mechanisms considered, contaminant pollution contributed the least to species models ( $1.4\% \pm 1.4\%$ ). With the exception of pollutant discharge (*DCP\_Discharge*), all disturbance predictors had non-zero influence for species models (Table A2 - 2).

Among family groups, the clearest differences we observed in terms of the contribution of disturbance mechanisms to species models were between cyprinids and salmonids. Species models for cutthroat trout and rainbow suggested that sedimentation is more influential (14.7% and 10.1%, respectively) for salmonids than for cyprinid species (6.36% for speckled dace; 0.8% for longnose dace). Sedimentation was most influential for mottled sculpin (cottid family, 15.7%) and less so for mountain sucker (catostomid family, 4.2%). Similarly, our models indicated that hydrologic alteration contributes more to the observed distribution of two cyprinid species (32.2% longnose dace; 7.2% speckled dace) than it does for either salmonid species (2.0% for cutthroat trout, 0.3% for rainbow trout).



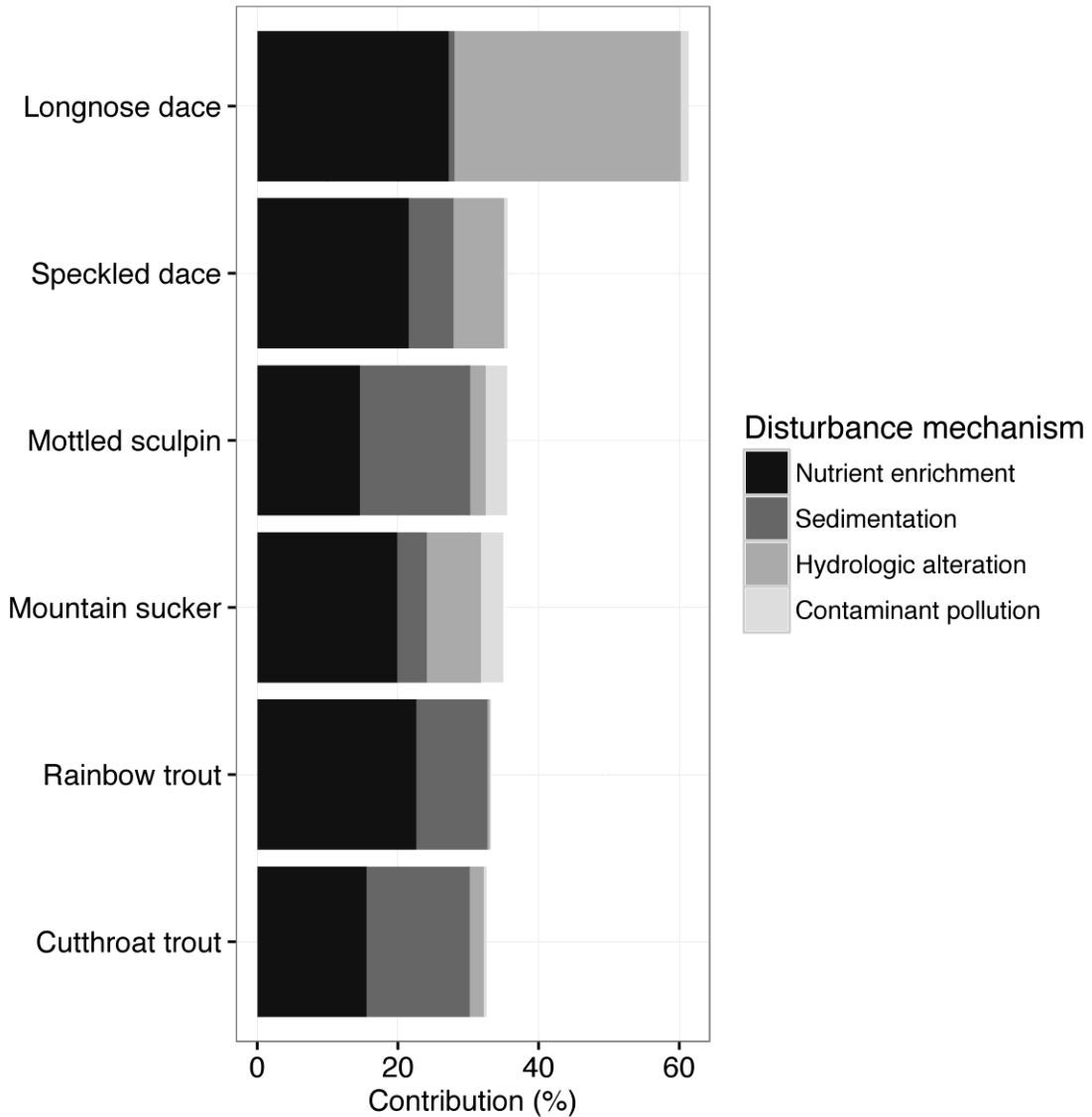


Figure 3-2. Contribution of anthropogenic disturbance mechanisms to models explaining contemporary species distributions. Contributions represent the sum of relative influence of anthropogenic predictors grouped by mechanisms of ecological influence (Allan, 2004). The relative influence of natural predictors (not shown) comprise the difference between the cumulative anthropogenic influence and 100%.

### 3.3.4 Species-environment relationships across broad environmental gradients

Partial dependence plots characterized differential responses for species across key environmental gradients. In the following section we interpret partial dependence plots for stream temperature to illustrate important differences in the response of all six fish species across a broad temperature gradient. To highlight ecological insights that can be obtained via a boosted

regression tree analysis, we also explore in more detail species-environment relationship across influential environmental gradients, focusing on a widely distributed species as an example. Deciles of predictors are represented as ticks along the x-axis and depict the distribution of occurrences along environmental gradients. Partial dependence plots may be noisy and complex in portions of environmental space where low density of observations occur (Leathwick *et al.*, 2008).

Although we restricted our analysis to fish species in cold (mottled sculpin, longnose dace, speckled dace, cutthroat trout, rainbow trout) and cool (mountain sucker) thermal guilds, we found that species exhibited unique thermal niches (Figure 3-3). Ranked from coolest to warmest thermal optima, we found substantial sorting among species: cutthroat trout (8 °C), mottled sculpin (12 °C), rainbow trout (15 °C), mountain sucker (16 °C), longnose dace (16 °C), and speckled dace (16.5 °C). Thermal niches also varied in terms of their range of suitable temperatures. For example, we found substantial differences between salmonid species, with cutthroat trout exhibiting a clear optimal temperature followed by a steep decline in occurrence probability to increasing temperatures. In contrast, peak occurrence probabilities for rainbow trout occurred over a broader range of temperatures (15 °C - 20 °C) and exhibited more modest declines in response to increasing temperatures in excess of 21 °C.

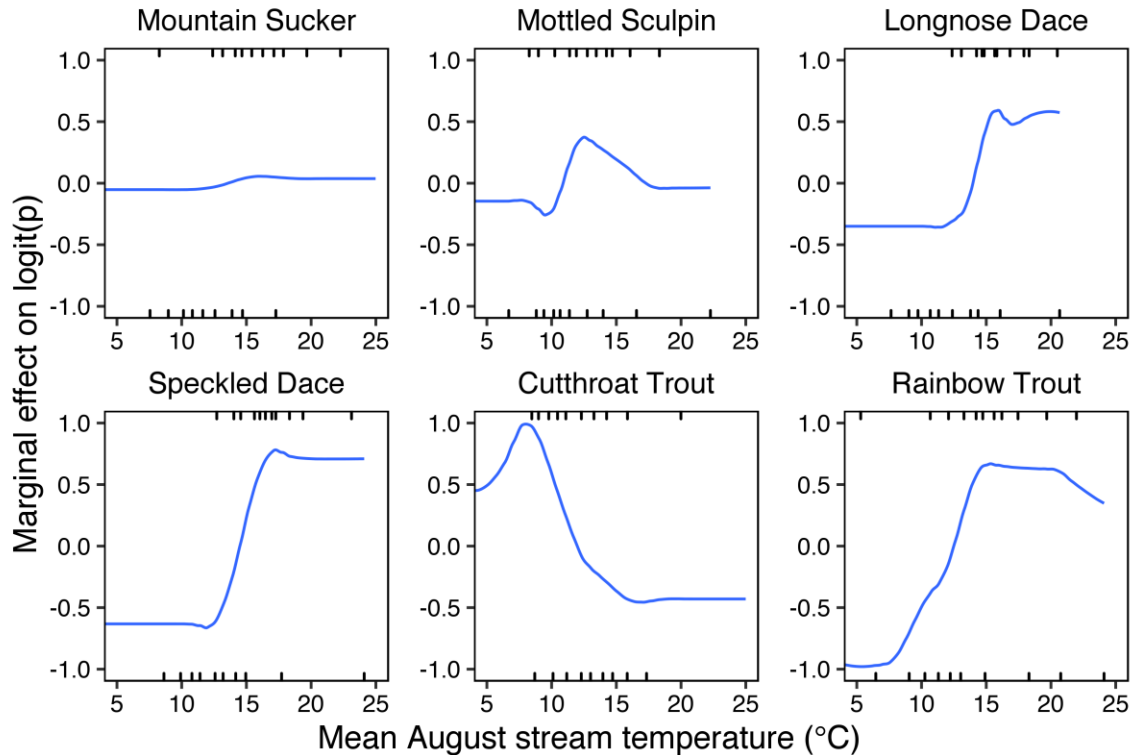


Figure 3-3. Partial dependence plots depicting thermal niches for five cold-water and one cool-water species. Plots depict relative probability of occurrence across a stream temperature gradient accounting for the average effects of all other predictors. Ticks at the top and bottom of each plot represent deciles of the predictor for species presences and absences, respectively, and are used to depict the distribution of occurrences along a stream temperature gradient. Y-axes are on the logit scale and are centered around the mean. Functions are plotted using a LOESS-smoothing span of 0.3.

We characterized the response of mottled sculpin across broad environmental gradients for its most influential predictors that included natural and anthropogenic variables. Figure 3-4 depicts non-linear relationships between mottled sculpin and the four most influential predictors. These predictors collectively describe aspects of hydrogeomorphic setting (mean annual runoff and slope) and disturbance gradients at catchment (cumulative nitrogen) and reach (substrate embeddedness) scales. Mottled sculpin occurrence peaks at relatively low stream gradients (~1%), declines along a gradient of increasing reach slope, and has a unimodal response along a gradient of increasing mean annual runoff (i.e. streamflow permanence), suggesting a high suitability of small streams.

## Mottled Sculpin

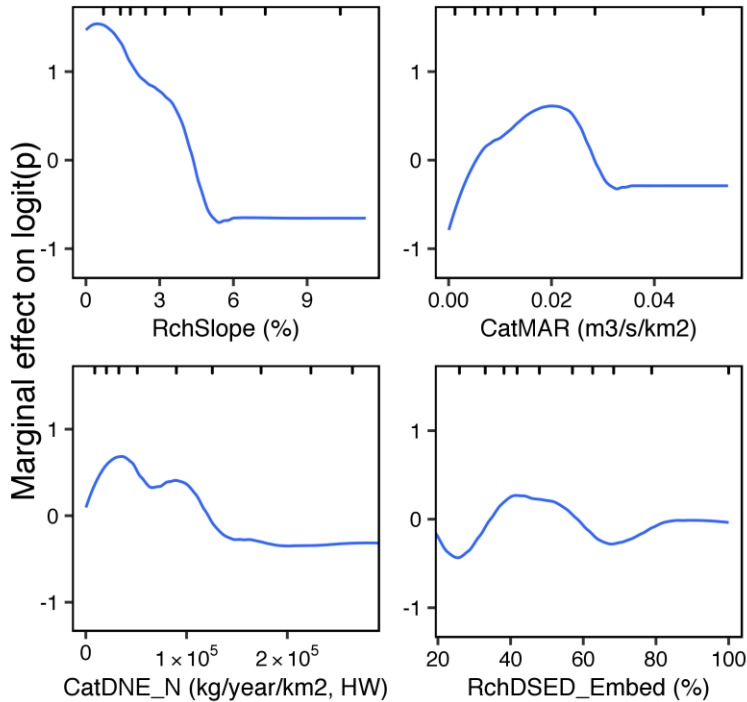


Figure 3-4. Partial dependence plots for the four most influential predictors of mottled sculpin occurrence. Plots illustrate how predicted probability of occurrence changes along key environmental gradients accounting for the average effects of all other predictors. Ticks at the top of each plot represent deciles of the predictor and are used to depict the distribution of occurrences along environmental gradients. Y-axes are centered around the mean. Functions are plotted using a LOESS-smoothing span of 0.3.

Human activities that deliver nitrogen to a stream appear to be a key driver of mottled sculpin occurrence throughout its historic range in the western United States. From the partial dependence plot we characterized that increasing nitrogen inputs were generally associated with a reduced probability of occurrence indicating that the species is less likely to occur in catchments with high nitrogen inputs *per unit area*, given the average effects of other modeled environmental predictors. Correlation between nitrogen and mean annual runoff was weak ( $r = 0.12$ ). The response along an embeddedness gradient was more complex but generally indicated that mottled sculpin occurrence peaks between 40%-50% and declines at higher levels of substrate impairment. Interpretation of a subsequent peak in partial dependence occurring at the high end of the embeddedness gradient (~90%) should be tempered by the low density of

observations occurring over the range from 80% - 100% embeddedness. Partial dependence plots for all species and predictors are provided in A.2. (see Figure A2 - 1 - Figure A2 - 6).

### *3.3.5 Interactions among environmental drivers*

Five of six species models included multiple interactions (i.e. boosted regression tree depth  $\geq 2$ ) indicating the presence of complex relationships between fish occurrence and environmental variables. We assessed the five strongest pairwise interactions modeled for each species for a total of 30 pairwise interactions. Interactions commonly involved a hydrogeomorphic predictor with baseflow occurring in 33.3% (10/30) of interactions and reach slope occurring in 23% (7/30) of interactions (Table 3-5).

Visualizing the effects of interacting predictors facilitates interpretation of species occurrence that varies jointly across multivariate environmental space. For instance, joint partial dependence plots can reveal synergistic as well as antagonistic effects as one moves across environmental gradients. Figure 3-5 illustrates a complex response surface for the strongest pairwise interaction detected among all species, an interaction between cumulative nitrogen and baseflow for cutthroat trout. The plot indicates that suitability for cutthroat trout is greatest in catchments with low to intermediate baseflow combined with relatively high nitrogen inputs from upland and atmospheric sources. Inspection of the interaction plots can also qualify interpretation of partial dependence on a single predictor – in this case, the apparent suitability of sites with high cumulative nitrogen inputs is tempered by an antagonistic effect of greater baseflows (i.e. increased groundwater contributions to discharge).

Table 3-5. The five strongest pairwise interactions between environmental predictors of cold-water and cool-water fish distribution are presented for each of the five species models for which interactions were supported. Interactions are presented in order of decreasing interaction strength as quantified using the H-index. Interaction strengths range between 0-1 with 1 being the strongest (Friedman & Popescu, 2008). Anthropogenic predictors are associated with disturbance mechanisms as follows: *DSED* = sedimentation, *DNE* = nutrient enrichment, *DCP* = contaminant pollution, *DHA* = hydrologic alteration. Note that *Cat* and *Rch* labels are excluded here. See Table 3-2 for full predictor abbreviations.

<b>Species</b>	<b>Variable 1</b>	<b>Variable 2</b>	<b>Interaction strength</b>
Cutthroat Trout	<i>Baseflow</i>	<i>DNE_N</i>	0.38
Cutthroat Trout	<i>Substrate</i>	<i>Baseflow</i>	0.29
Mountain Sucker	<i>Baseflow</i>	<i>Slope</i>	0.23
Rainbow Trout	<i>Substrate</i>	<i>Riparian</i>	0.22
Mountain Sucker	<i>Baseflow</i>	<i>DHA_Canals</i>	0.20
Mountain Sucker	<i>Riparian</i>	<i>DSED_Sediment</i>	0.20
Mottled Sculpin	<i>Substrate</i>	<i>DNE_N</i>	0.19
Cutthroat Trout	<i>StreamT</i>	<i>DNE_N</i>	0.19
Speckled Dace	<i>StreamT</i>	<i>Slope</i>	0.19
Cutthroat Trout	<i>Baseflow</i>	<i>DSED_Embed</i>	0.18
Mountain Sucker	<i>MAR</i>	<i>Slope</i>	0.15
Mottled Sculpin	<i>DSED_Sediment</i>	<i>Slope</i>	0.15
Mottled Sculpin	<i>StreamT</i>	<i>Baseflow</i>	0.14
Cutthroat Trout	<i>Baseflow</i>	<i>DSED_Sediment</i>	0.14
Rainbow Trout	<i>Confine</i>	<i>DSED_Sediment</i>	0.13
Mountain Sucker	<i>Confine</i>	<i>DNE_N</i>	0.13
Mottled Sculpin	<i>Substrate</i>	<i>Slope</i>	0.13
Mottled Sculpin	<i>StreamT</i>	<i>MAR</i>	0.13
Rainbow Trout	<i>Riparian</i>	<i>DSED_Embed</i>	0.12
Speckled Dace	<i>DHA_FlowMod</i>	<i>Slope</i>	0.11
Rainbow Trout	<i>Baseflow</i>	<i>Slope</i>	0.11
Rainbow Trout	<i>StreamT</i>	<i>Substrate</i>	0.11
Speckled Dace	<i>DSED_Embed</i>	<i>DNE_N</i>	0.10
Speckled Dace	<i>Baseflow</i>	<i>DNE_N</i>	0.10
Speckled Dace	<i>RchRiparian</i>	<i>Baseflow</i>	0.09

The potential for negative synergistic interactions reinforces the need to consider species-environment relationships across broad gradients to capture nonlinearities that occur among key drivers of species occurrence and to assess their joint influences. As an illustration, we analyzed the joint partial dependence of rainbow trout on two interacting predictors - riparian vegetation cover and substrate embeddedness, a measure of substrate quality associated with anthropogenic

disturbance. Figure 3-6 depicts a synergistic interaction for rainbow trout that consists of a negative relationship to increasing density of riparian vegetation above moderate levels of cover that is intensified at high levels of embeddedness.

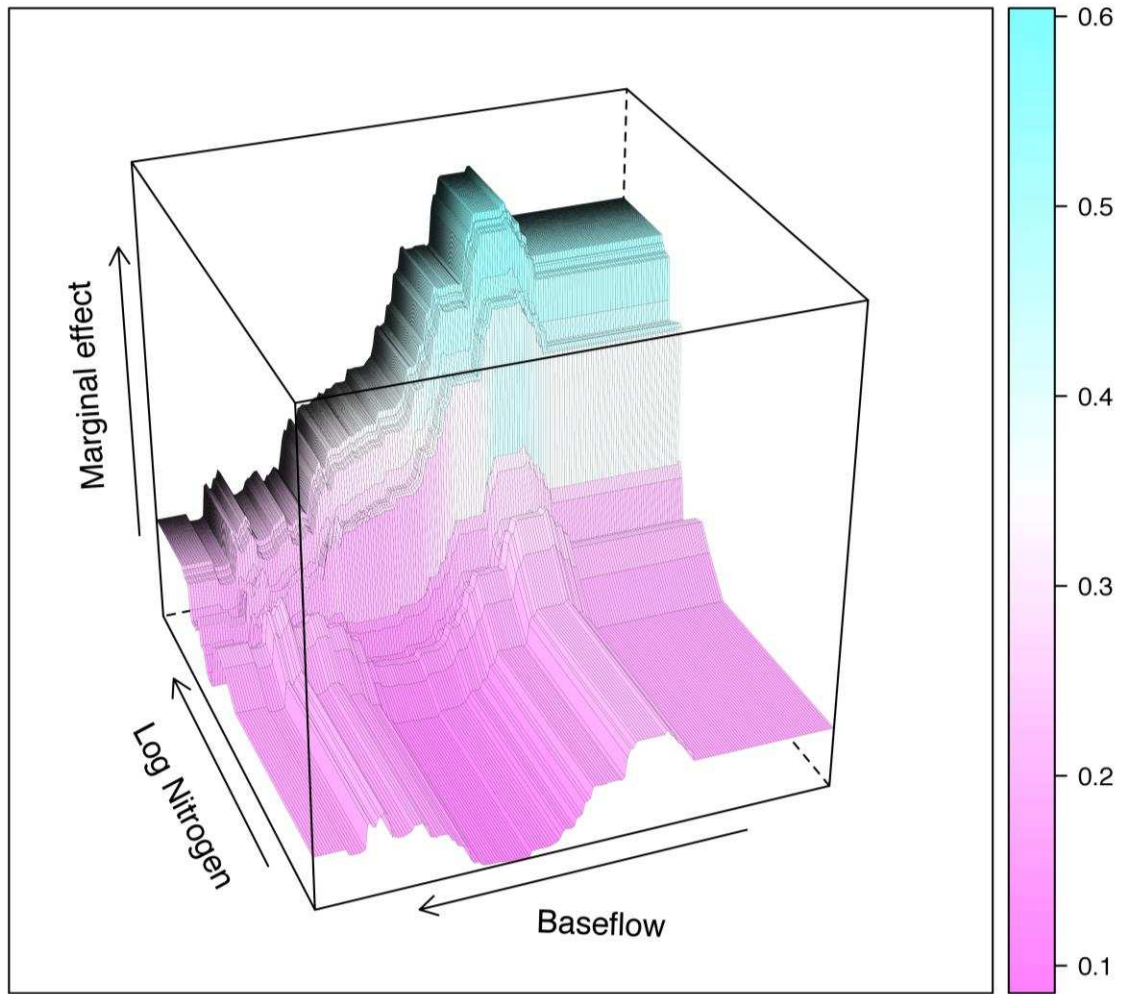


Figure 3-5. Joint partial dependence plot illustrating an antagonistic interaction involving an anthropogenic disturbance (nitrogen) and baseflow for cutthroat trout – the strongest of all interactions detected (Table 3-5). Suitability to high nitrogen inputs is reduced by increasing baseflows. Arrows along axes indicate the direction of increasing values. The z-axis corresponds to the marginal effect or partial dependence of cutthroat trout occurrence on log nitrogen and baseflow given the average effects of other predictors in the species model. Colors represent the marginal effect in terms of predicted probability of occurrence (0-1) as indicated in color scale bar.

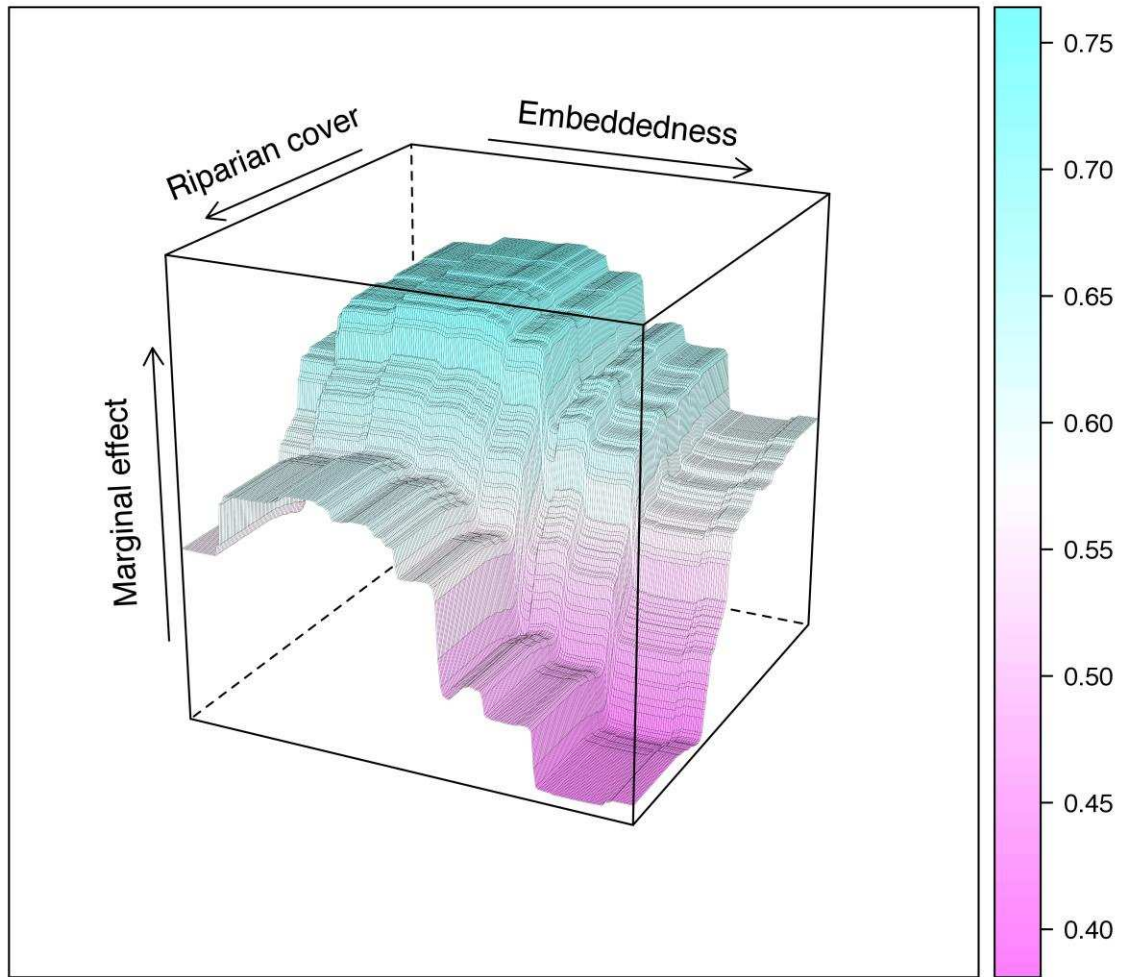


Figure 3-6. Joint partial dependence plot for rainbow trout depicting a synergistic interaction between density of riparian cover and substrate embeddedness. The surface indicates a negative relationship between rainbow trout occurrence and high densities of riparian cover that is exacerbated by impaired substrate quality. Arrows along axes indicate the direction of increasing values. The z-axis corresponds to the marginal effect or partial dependence of rainbow trout occurrence on riparian cover and embeddedness given the average effects of other predictors in the species model. Colors represent the marginal effect in terms of predicted probability of occurrence (0-1) as indicated in color scale bar.



### 3.4. Discussion

To characterize contemporary drivers that shape the distributions of cold- and cool-water fish species, we modeled species occurrence across a full spectrum of natural and disturbance gradients, accounting for the pervasive influences of land use (Allan, Erickson & Fay, 1997) and hydrologic modifications (Grill *et al.*, 2015). We focused explicitly on summer stream temperature as a key climatic variable because it sets thermal limits on the distribution of cold- and cool-water fishes (Eaton *et al.*, 1995; Rahel, 2002; Roberts *et al.*, 2013).

#### 3.4.1 Natural drivers of species distribution

We identified several natural and anthropogenic environmental variables as among the key drivers of the occurrence of cold- and cool-water riverine species in the western United States. We found that stream gradient, mean annual runoff, and baseflow were influential contributors to our models of species occurrence, highlighting the role of the geomorphic template and regional climate in influencing stream ecology and the distribution of fish species. These findings are congruent with the conceptualization of streams as hierarchical systems whose distribution of habitats and associated biota can be thought of in terms of an array of influences operating over multiple spatial and temporal scales (Frissell *et al.*, 1986; Tonn, 1990; Poff, 1997).

Not surprisingly, we found that August stream temperature consistently ranked among the most influential predictors for all six species analyzed here. We did, however, characterize important differences in species' thermal niches that reveal ecological insights about thermal suitability across a broad range of stream temperature. For example, comparison of thermal niches for the two species of salmonid indicates that rainbow trout occupy a warmer and broader range of stream temperatures than do cutthroat trout. In addition, speckled dace exhibited only marginal declines in occurrence at the upper end of the stream temperature gradient, indicating a

larger thermal niche breadth than for mottled sculpin whose occurrence was more sensitive to increases in temperature above its optima. As an informal validation, we compared our thermal niches that were based on partial dependence plots to those generated via an independent study involving cold-water fishes in Oregon (Huff, Hubler & Borisenko, 2005) and found consistency in terms of species' relative rankings both for temperature optima and niche breadth. We believe that boosted regression tree analysis offers researchers a meaningful and accessible method for characterizing ecological niches precisely because partial dependence plots are well-suited to examine species response along environmental gradients (Zurell, Elith & Schröder, 2012).

In addition to summer stream temperature, we recognize that other climate variables including winter temperatures and seasonal precipitation are likely to constrain the distribution of freshwater fishes (Poff *et al.*, 1997; Jackson, Peres-Neto & Olden, 2001; Wenger *et al.*, 2011). However, to the degree that the occurrence of cold-water fish is influenced by maximum stream temperature, their distribution is likely to become increasingly constrained under a warming climate. Given that GCM projections on the directionality and magnitude of temperature change tend to converge for our study area (Walsh *et al.*, 2014), increased future stream temperatures are likely.

### *3.4.2 Anthropogenic drivers of species distribution*

To capture a broad range of anthropogenic influences that exist in rivers and streams throughout the western United States, we evaluated drivers of native cold- and cool-water fish occurrence corresponding to several key gradients of human influence. Disturbance mechanisms played an important role in the occurrence of all six fish species with anthropogenic variables accounting for roughly one third to nearly two thirds of model outcomes. Nutrient enrichment, sedimentation, and hydrologic alteration were the most influential mechanisms and are commonly cited among the leading sources of impairment for stream and river systems

worldwide (Malmqvist & Rundle, 2002; Allan & Castillo, 2007; Strayer & Dudgeon, 2010). Freshwater biota face numerous additional threats to those we have quantified here (Dudgeon *et al.*, 2006) including exotic species and depletion of surface water that have been recognized as among the leading anthropogenic threats to fish species in the western US (Richter *et al.*, 1997). However, given our objective to establish mechanistic linkages between human activities and stream conditions that affect fish occurrence, we did not intend for this assessment to be an exhaustive treatment of all stressors. We therefore acknowledge that our estimates of the relative contribution of anthropogenic influence to contemporary fish distributions are likely to be conservative in that they do not account for additional factors responsible for historic and ongoing species' range reductions.

We found that species respond differentially to stressors, with some species having greater sensitive to environmental change than others. This finding is supported by previous research (Carlisle & Hawkins, 2008) and can be understood in terms of traits that predispose species to particular environmental conditions. For instance, because their life history requires suitable substrate for spawning and embryo survival (Irving & Bjornn, 1984), salmonids are particularly susceptible to sedimentation (Young, 1995). Efforts to group species by reproductive behavior (i.e. spawning guild) have supported the generalization that fishes that do not clean silt from their nests are sensitive to sedimentation (Jones III *et al.*, 1999). Trout species and longnose dace are among these sensitive species. Conversely, nest excavating cyprinid species and nest guarding cottids (mottled sculpin) that use fanning behavior to regulate sediment in nests and oxygenate their eggs appear to be more tolerant of sediment-disturbed streams (Sutherland, Meyer & Gardiner, 2002; Helfman *et al.*, 2009; Kemp *et al.*, 2011).

We found that nutrient enrichment in the form of cumulative nitrogen was the single most influential anthropogenic predictor of cold- and cool-water fish species occurrence, a sign of the pervasiveness of human influence on the chemistry of flowing waters of the western United States. This influence is also felt globally, with previous estimates indicating that greater than 90% of rivers worldwide have nitrate concentrations exceeding pristine levels (Heathwaite, 1996). Across a gradient of increasing nitrogen we modeled consistent declines in species occurrence that suggest that cold- and cool-water fish are sensitive to nitrogen inputs (see Figure A2 - 1). Although studies investigating direct effects of nutrients on primary productivity and indirect effects on primary and secondary consumers are numerous, there are comparatively few observational studies on direct linkages between nutrients and fish assemblages (Wang *et al.* 2007). In their analysis of biotic assemblages in wadeable streams of Wisconsin, Wang, Robertson and Garrison (2007) found significant associations between nutrients and fish assemblages including negative correlations involving total phosphorus and total nitrogen with the abundance of salmonids as well as with other measures of intolerant fish species. Direct impacts to fish are also possible from the proximate causes of nutrient enrichment that include agriculture, industrialization, and urbanization (Wang & Lyons, 2003).

One notable exception to our finding that fish occurrence responded negatively to nitrogen inputs was for cutthroat trout whose response to increasing nitrogen was inconsistent across the gradient, consisting of multiple peaks (Figure A2 - 1 - Figure A2 - 6). Characterization of a complex response to nitrogen inputs likely reflects additional environmental influences, thereby challenging direct interpretation of nitrogen's influence on cutthroat trout occurrence. For example, the presence of antagonistic interaction between nitrogen and baseflow (Figure 3-5) indicates an overriding influence of groundwater inflows. High baseflow provides thermal

stability through buffering of cool groundwater inputs (Poole & Berman, 2001; Caissie, 2006) and is indicative of stable flow environments (Rieman & Isaak, 2010). Stable flow environments and those with infrequent spring and summer flooding events have been found to contribute to invasion success of rainbow trout (Fausch *et al.*, 2001; Wenger *et al.*, 2011) whose introduction has been detrimental to cutthroat trout distribution (Behnke, 2002). Although biotic interactions were beyond the scope of this analysis and were not assessed, we would expect that multiple drivers are likely to influence fish occurrence. Furthermore, we believe that evaluation of interactions between drivers may provide insight into species response in ways that can disentangle complex environmental relationships.

### *3.4.3 Implications for climate warming*

In addition to explaining contemporary species distributions, two properties of species' ecological niches (Schoener, 1989) can offer insights on potential effects of climate warming. First, niche position may inform understanding of a species' sensitivity to climate warming by providing an indication of where optimal temperatures fall in relation to existing or future temperature gradients. Marginal niche positions are those that deviate far from mean conditions, suggesting susceptibility to unidirectional environmental change such as climate warming (Thuiller, Lavorel & Araujo, 2005). In addition, niche breadth can inform *a priori* classification of the relative sensitivity of species to warming. For example, species with narrow thermal niches are expected to be more sensitive to climate warming than species with broad niches (Poff, Olden & Strayer, 2012; Botts *et al.*, 2013; Heino *et al.*, 2015). However, there is recent evidence that headwater streams are buffered from warming, minimizing the amount of exposure faced by cold-water specialists in small mountain streams (Isaak *et al.*, 2016).

A caveat of observational studies is that characterization of species' environmental niches using empirical approaches like those employed here is dependent on multiple factors that

influence how closely approximation of the realized niche reflects the fundamental niche (Colwell & Rangel, 2009). Two key factors are: 1. How much of the full environmental gradient is captured in the analysis? 2. To what degree does the distribution of presences and absences reflect phenomena not included in the species distribution model? Because the aim of this study was to assess contemporary drivers of fish species occurrence, we sought to expand on the reference approach to include sites covering a full range of environmental conditions ranging from reference to disturbed. Our use of data obtained through westwide and national surveys conducted using a random sampling design is a key feature of this analysis that enabled us to capture broad environmental gradients that exist within species' historic native ranges.

In regards to the second factor, we explicitly assessed anthropogenic influences that could potentially account for much of the contemporary patterns of species distribution beyond that attributable to natural environmental variation. We did this by incorporating a diverse suite of anthropogenic influences as predictors for our species distribution models using a mechanistic framework to link human activity to ecologically meaningful endpoints. To account for potential biases in occurrence data that would result from including presences attributable to human introduction, we excluded observations occurring outside of species' historic native ranges. Thus, although we attempted to account for species introductions by restricting geographic extent, biotic interactions with introduced fish species were beyond the scope of this analysis and were not explicitly modeled.

Introduction of nonnative salmonids throughout the former range of cutthroat trout began at the turn of the nineteenth century (Behnke, 1992). Establishment of non-native salmonids and subsequent interaction with cutthroat trout through a variety of mechanisms have been implicated in the decline of cutthroat trout populations throughout the western United States

(Krueger & May, 1991; Dunham *et al.*, 2002). Chief among these mechanisms are loss of genetic variation through hybridization with rainbow trout (Duff, 1988; Muhlfeld *et al.*, 2009; Penaluna *et al.*, 2016), competition and predation by brook trout (*Salvelinus fontinalis*) and competition with brown trout (*Salmo trutta*) (Fausch, 1988; Quist & Hubert, 2004; McHugh & Budy, 2011). The degree to which biotic interactions involving nonnative salmonids may have historically displaced cutthroat trout from sites that were otherwise potentially suitable and thus contributed to the narrow thermal niche we characterized for cutthroat trout is unknown. However, a study by Wenger *et al.* (2011) found biotic interactions to be an important driver of cutthroat trout distribution, reporting that the presence of non-native species accounted for a 26% reduction in distribution of cutthroat trout throughout its historic range.

Findings from our range-wide analysis, however, can be interpreted with the aid of experimental studies that measure species physiological performances under controlled conditions to explain the ability of rainbow trout to displace cutthroat at warmer, low elevation stream reaches and to account for the limited overlap we observed in their thermal niches. For example, an experimental study involving westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), a subspecies of cutthroat, found that rainbow trout maintain physiological advantages (i.e. greater survival and growth) at warm temperatures (Bear, McMahon & Zale, 2007). Given these considerations, we advise caution when attempting to infer species' thermal limits from thermal niches that are generated from observed distribution patterns because occurrences may reflect effects of competitive displacement, anthropogenic activities, or dispersal limitations as opposed to purely climatic determinants (Rahel, 2002; Colwell & Rangel, 2009).

#### 3.4.4 Interactions

We detected interactions among environmental variables, thereby identifying complex relationships between the drivers of species occurrence. Importantly, we found that human

pressures do not operate in isolation, in many cases exerting joint influence along with other environmental factors. The potential for interactions to drive species responses in complicated and important ways indicates the need to account for joint influences in assessing environmental relationships. For example, we detected an interaction for rainbow trout between riparian cover and substrate embeddedness, suggesting a complex interplay between riparian and in-stream habitat (Figure 3-6). Above moderate densities of riparian vegetation cover we characterized a positive association of rainbow trout occurrence to decreasing cover that depends on accumulation of fine sediments. Interactions between riparian cover and sediment for stream biota were previously reported by Hawkins *et al.* (1983) who observed that differences in the density of total stream vertebrate species between sites with and without riparian shading increased along a gradient of fine sediment. They viewed this phenomenon as a trade-off between increases in invertebrate food base and decreases in habitat quality via accumulation of fine sediment that arise from the clearing of riparian canopy.

It is interesting to consider that not all species would respond positively to increased density of riparian cover and that species-specific benefits may depend on additional interacting factors. Human activities that result in thinning or loss of riparian cover have been implicated in numerous environmental impacts including downstream increases in stream temperature, loss of woody debris, impacts to terrestrial invertebrate assemblages, and impairment of water quality (Cummins *et al.*, 1989; Castelle, Johnson & Conolly, 1994; Waters, 1995; Naiman & Decamps, 1997). Reduced density of riparian cover can, however, increase solar insolation in streams which may in turn stimulate primary production and enhance autotrophic food supply for salmonids (Murphy, Hawkins & Anderson, 1981; Bilby & Bisson, 1987; Li *et al.*, 1994). Platts and Nelson (1989) posited that benefits to salmonids of increased invertebrate abundance could



be outweighed by increased stream temperature, although the effect of riparian vegetation loss on stream temperature may depend on topographic aspect (Li *et al.*, 1994). Riparian vegetation is likely to be an important factor for the persistence of cold-water species under climate warming. For example, modeling work by Lawrence *et al.* (2014) suggests that extirpation of salmonid species may in some cases be prevented through restoration of riparian vegetation that regulates stream temperature and indirectly inhibits expansion of nonnative fish species.

#### *3.4.5 Management implications*

At a regional scale, contemporary distributions of cold- and cool-water fish species appear to be driven to a substantial degree by human activities. Of concern to fish conservation is that anthropogenic influences are likely to become stronger in an increasingly modified world (Heathwaite, 2010; Olden *et al.*, 2010; Comte *et al.*, 2013; Theobald & others, In prep). We suggest that future efforts to model species distributions incorporate human activities through a mechanistic lens to provide ecological insight into various disturbance pathways. For example, we found that sedimentation was influential in shaping species distributions with variation in modeled contribution explained through ecological traits. Sedimentation was highly influential for cutthroat trout and rainbow trout, salmonids whose spawning requirements make them sensitive to sedimentation processes that impair substrate. Mottled sculpin were strongly influenced by sedimentation, but were positively associated to a gradient of increasing sedimentation, a finding that may be attributed to their ability to behaviorally regulate their spawning environment. Hydrologic alteration, a common symptom of managed river systems (Bunn & Arthington, 2002; Nilsson *et al.*, 2005; Dudgeon *et al.*, 2006; Poff & Zimmerman, 2010), was most influential for longnose dace, speckled dace, and mountain sucker. Numerous ecological impacts are associated with dams and reservoir operations whose other major impacts

include fragmentation of river networks (Grill *et al.*, 2015) and alteration of thermal (Caissie, 2006) and sediment regimes (Wohl *et al.*, 2015).

Characterization of mechanisms by which human activities influence fish species is valuable for identifying management actions that can deliver desired ecological benefits most efficiently. For instance, the re-establishment of riparian vegetation can address multiple stressors on stream condition by buffering nutrient and sediment flows, by insulating stream temperature through shading, by contributing organic material including woody debris to streams, and by providing habitat to diverse species (Gregory *et al.*, 1991; Naiman & Decamps, 1997; Poole & Berman, 2001; Lake, Bond & Reich, 2007; Lawrence *et al.*, 2014). Knowledge of the causes of habitat impairment is further needed to identify relevant scales for stream management (Esselman *et al.*, 2011) because upstream processes may overwhelm localized management efforts and riparian functions at the reach scale (Roth, Allan & Erickson, 1996; Wang, Robertson & Garrison, 2007). Thus, a guiding criteria for stream restoration should be to target actions that are commensurate with the scale of the underlying causes of habitat impairment (Jones III *et al.*, 1999; Beechie *et al.*, 2010). Our identification of sedimentation and nutrient enrichment as primary anthropogenic drivers suggests that systematic watershed planning may be a necessary complement to reach-scale habitat improvements such as those provided by riparian restoration (Nel *et al.*, 2009). Managing the natural infrastructure of catchments to provide hydrologic ecosystem services including regulation of nutrient and sediment yields is an emerging strategy for delivering multiple benefits (Brauman *et al.*, 2007; Harrison-Atlas, Theobald & Goldstein, 2016).

Importantly, we found that species had variable responses across gradients of anthropogenic stressors, suggesting that future efforts consider expanding the reference approach

to capture important features like local optima, thresholds, and interactions whose detection requires assessment of continuous gradients. Findings from reference sites will continue to offer important ecological insights (e.g. Pyne & Poff, 2016), but may be less relevant to management concerns that continue to mount with the addition of multiple human pressures (Strayer & Dudgeon, 2010). The looming threat of climate change necessitates that approaches to freshwater conservation consider anthropogenic and climate-related stressors among the broad suite of potential environmental changes to anticipate likely impacts to species' geographic ranges. Forward looking adaptation strategies to protect climate refugia (Isaak *et al.*, 2015) and facilitate climate-induced dispersal by improving habitat connectivity will be required under a non-stationary climate (Schmitz *et al.*, 2015). To support climate adaptation, there is an urgent need for research to inform the vulnerability of freshwater systems to climate change (Buisson & Grenouillet, 2009; Olden *et al.*, 2010; Strayer & Dudgeon, 2010) and to address key knowledge gaps including interactions between climatic and anthropogenic stressors and effects of invasive species (Olden *et al.*, 2010).

Looking forward, we anticipate that developing a quantitative basis for how fish species respond to anthropogenic stressors and climate drivers across gradients of natural variation will be key to their conservation and management. As global change continues to shape the landscapes that influence river systems, disentangling the contemporary drivers of fish species distribution will be needed to inform conservation planning with credible and salient information. We believe that progress in freshwater conservation requires understanding of disturbance mechanisms, interactions among stressors, and detection of nonlinear responses as we have demonstrated here.

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## **4 Translating future climate exposure into range-wide and site-level vulnerability for native salmonids of the western United States**

### **4.1. Introduction**

Freshwater ecosystems are among the most imperiled worldwide with species facing disproportionate risk of extinction compared to other forms of biodiversity (Ricciardi & Rasmussen, 1999; Strayer & Dudgeon, 2010). Assessing changes to the distribution of freshwater fishes has become a priority area for research and conservation (Olden *et al.*, 2010) since stream organisms are considered uniquely vulnerable to climate change (Buisson *et al.*, 2008; Isaak & Rieman, 2013) and are threatened by numerous additional human stressors (Dudgeon *et al.*, 2006) including habitat fragmentation (Nilsson *et al.*, 2005) that is likely to limit opportunities for dispersal in a changing environment (Woodward, Perkins & Brown, 2010). Quantifying this vulnerability, however, presents a major challenge given inherent difficulties in modeling of climate projections and species response (Poff, Olden & Strayer, 2012) and the need to account for additional environmental influences that are likely to shape local responses (Isaak *et al.*, 2012).

Fish species have frequently served as model organisms for understanding the effects of climate change on freshwater ecosystems with many foundational studies relying on established thermal tolerances as a way to assess impacts of a warming climate (Eaton & Scheller, 1996; Keleher & Rahel, 1996; Mohseni, Stefan & Eaton, 2003; Table 4-2). Broad-scale studies have been influential in shaping regional views of climate vulnerability yet depend on generalized relationships between climate warming and fish distributions. Accurate assessment of thermally suitable habitat is essential for projecting species response to climate change (Caissie, 2006; Ficklin *et al.*, 2014) but has been challenging at large spatial extent. Most broad-scale studies

have inferred climate impacts based on relatively crude approximations of warming, for example, by using coarse-resolution climate projections (e.g. Eaton & Scheller, 1996; Mohseni, Stefan & Eaton, 2003), applying universal temperature increases across broad geographies (Keleher & Rahel, 1996), and commonly using air temperature as a surrogate for stream temperature (e.g. Eaton & Scheller, 1996; Keleher & Rahel, 1996; Williams *et al.*, 2009; Wenger *et al.*, 2011) that may be unreliable given that streams are differentially sensitive to increases in air temperature (Wu *et al.*, 2012; Luce *et al.*, 2014; Isaak *et al.*, 2016). In recent years, studies have become progressively more sophisticated in their analyses of stream temperature and have trended towards the use of high resolution datasets (Landguth *et al.*, 2014; Isaak *et al.*, 2015); however, to date there is limited application of stream temperature data to assess climate vulnerability across broad spatial extent.

Most studies of projected shifts in fish distributions have considered climate to be a key global change driver of fish species response and have evaluated future effects largely independent of non-climatic stressors (Comte *et al.*, 2013; Matthaei & Lange, 2015). Comte *et al.* (2013) found that the magnitude and variability of *observed* climate effects exceeded that of *projected* climate effects and concluded that other drivers are likely responsible in addition to climate. Some researchers have even considered a narrow focus on climate change to be a distraction from other important drivers of species loss, citing that over 85% of published studies on biodiversity impacts of global change examined only climate change effects (Titeux *et al.*, 2016). For example, stream ecosystems are greatly affected by land use influences that include sedimentation, nutrient enrichment, hydrologic alteration, contaminant pollution, and riparian clearing (Allan, 2004).

These influences represent major drivers of contemporary freshwater fish distributions (Harrison-Atlas, Poff & Theobald, In prep.) and are likely to interact with climate change to affect species' vulnerability (Nelson *et al.*, 2009). The presence of multiple, interacting stressors that include emerging climate and anthropogenic drivers heightens the need to account for the broader context of human activities (Steen, Wiley & Schaeffer, 2010; Wiley *et al.*, 2010) in quantification of threats to freshwater biota. There are also several practical reasons to broaden assessments of vulnerability to include the influence of additional stressors and to examine potentially beneficial adaptation strategies. For instance, including stressors can improve the reliability of results (Filipe *et al.*, 2013) and can enrich understanding of potential effects of global change (Nelson *et al.*, 2009). Moreover, knowledge of interactive effects between climate and other environmental stressors is increasingly needed to support climate adaptation and freshwater management in contexts that must also contend with these legitimate additional pressures (Domisch *et al.*, 2015; Kuemmerlen *et al.*, 2015). Given the ubiquitous transformation of the natural landscape and river systems by human activities (Allan & Castillo, 2007), and impending yet uncertain climate change, there is a need for studies that can assess vulnerability over a wide range of environmental conditions and can establish linkages to climate adaptation to support management in the face of uncertainty.

Our aims in this study were to evaluate the range-wide vulnerability of cold-water fish species to projected climate change in the western United States and to assess site-level vulnerability to varying degrees of climate exposure and local environmental conditions. We focused on cold-water species whose presumed sensitive to warming at range margins and at elevation margins common in the montane West allows exploration of interactions between temperature and land use. Towards these complementary aims, we examined the following

research questions: (1) How will projected climate change, in particular through changes in stream temperature and streamflow, influence the range-wide vulnerability of native cold-water fish species across the western United States? (2) What effect will changes in climate and land use have on site-level vulnerability? (3) What is the potential of climate adaptation measures to mitigate vulnerability to climate change?

To address these questions, we conducted a suite of analyses to model range-wide and site-level vulnerability of native salmonid species in the western United States for 2040 and 2080. We assessed species' range-wide vulnerability by quantifying changes in suitable habitat as a function of projected stream temperature and streamflow to assess independent effects of climate change. Recognizing that climate change projections remain uncertain, particularly with respect to hydrology, and are likely to interact with additional stressors, we conducted a complementary set of analyses using a decision-scaling approach to explore vulnerability for plausible climate and land use futures while addressing uncertainty in modeled projections (Brown *et al.*, 2011). In this second set of analyses, we focused on a subset of sites representative of natural and anthropogenic gradients that exist in the western United States to incorporate fine-scale environmental variables to examine vulnerability across scenarios for key stressors and climate adaptation strategies.

We focused specifically on summer stream temperature due its recognized influence on the distribution of freshwater fish (Rahel, 2002). Since 1980, stream temperatures have increased by  $> 0.2$  °C/decade on average over the northwestern United States (Isaak *et al.*, 2012). Changes in precipitation patterns and streamflow have also been observed (Barnett *et al.*, 2008) and are likely to continue under climate change (Elsner *et al.*, 2010), although projections for precipitation are less certain than they are for temperature (Christensen *et al.*, 2007; Mote &

Salathé, 2010). Therefore, we also considered scenarios of altered flow due its ecological significance in rivers and streams (Power *et al.*, 1995; Poff *et al.*, 1997) and because of its sensitivity to changes in climate (Stewart, Cayan & Dettinger, 2005). These changes are particularly relevant for snowmelt-dominated systems (Barnett *et al.*, 2004; Fritze, Stewart & Pebesma, 2011) that are common among montane regions in the western United States.

We focused on rainbow trout (*Oncorhynchus mykiss* sp.) and cutthroat trout (*Oncorhynchus clarkii* sp.) -- two wide-ranging salmonids of significant conservation and economic importance (Harris, 2010; Loomis & Ng, 2012). Although widely introduced throughout the United States, many populations of rainbow trout including coastal (*O. mykiss irideus*) and interior forms occurring east of the Cascade Range and Sierra Nevada (commonly referred to as redband trout) have been threatened throughout their native range (Muhlfeld *et al.*, 2015). Aside from lake trout (*Salvelinus namaycush*), cutthroat trout historically occupied the largest geographic range of all salmonids in North America. The introduction of nonnative salmonids in tandem with other deleterious human activities has affected cutthroat throughout their range, greatly reducing their current distribution (Behnke, 2002). Presently, several subspecies of cutthroat trout are considered threatened or endangered while others have gone extinct (Penaluna *et al.*, 2016).

Despite their association as cold-water species, cutthroat trout and rainbow trout exhibit unique thermal optima (Bear, McMahon & Zale, 2007). In addition, cold-water species possess varying thermal niche breadth (Harrison-Atlas, Poff & Theobald, In prep.) that may indicate susceptibility to climate change. For example, species with narrow niche breadth are likely more vulnerable to environmental change (e.g. climate warming; Poff, Olden & Strayer, 2012; Heino *et al.*, 2015). To our knowledge, this is the first study to assess projected climate impacts over

species' native geographic ranges using high-resolution stream temperature and streamflow data. Moreover, we know of no other studies that have assessed site-level vulnerability of fish species across plausibly diverse climate trajectories and for alternative land use scenarios.

## **4.2. Methods**

We obtained stream survey data from regional (Western Environmental Assessment and Monitoring Program; WEMAP) and national (National Rivers and Streams Assessment; NRSA) surveys conducted by the U.S. Environmental Protection Agency (EPA, 2006; EPA, 2016). Survey sites were stratified by state and were selected using a probability based sample design (Stevens & Olsen, 2004) to sample streams that ranged in size between Strahler first order streams and large rivers. Methods for fish sampling varied by stream size. Surveys employed backpack electrofishing in third-order and smaller streams and utilized raft electrofishing in fourth-order and larger rivers (Whittier *et al.*, 2007). We compiled information from fish surveys on the occurrence of rainbow trout and cutthroat trout by converting measures of abundance into presence/absence at each sample site (Leathwick *et al.*, 2005). We focused on sites within historic native geographic ranges (Table 4-1) that were delineated at the subbasin scale (8-digit US Geological Survey hydrologic unit codes) according to expert knowledge and historical records (NatureServe, 2010). Reach-level measures of woody riparian vegetation cover (% areal cover) and substrate embeddedness (%), a measure of the fraction of a particle's surface surrounded by fine sediments, were taken from the surveys. The metric for riparian cover characterizes ground, mid-, and canopy layers and is relevant for assessing potential shading of streams (Kaufmann *et al.*, 1999). Riparian cover and embeddedness were estimated systematically using consistent protocols under both WEMAP and NRSA surveys (Kaufmann *et al.*, 1999; EPA, 2007). Measurements of embeddedness were deemed sufficiently precise for this

analysis (see Supporting Information in A.2.) and compare favorably to other substrate metrics in terms of their reliability and relevance for this study.

Table 4-1. Native salmonid species included in this analysis. Prevalence indicates the proportion of sites within the native range where a species was detected. Due to geographic overlap that exists between species' native ranges, some survey sites (n=167) were used in assessments for both species.

Common name	Genus and species	Survey sites	Prevalence
Cutthroat trout	<i>Oncorhynchus clarkii</i>	356	0.26
Rainbow trout	<i>Oncorhynchus mykiss</i>	300	0.63

Stream sampling occurred primarily during summer months when stream temperatures are warmest. We acquired modeled stream temperature data from the NorWeST collaborative effort ([www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html](http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html)) that combined an extensive collection of stream temperature observations from more than 20,000 sites across the West with a spatial-statistical modeling approach (Isaak *et al.*, 2014) to produce accurate stream temperature estimates ( $r^2 \sim 0.9$ ). Spatial dependence of stream temperature is modeled using autocovariance functions to account for spatial autocorrelation in stream networks. We used mean August stream temperature (1993-2011) as our baseline temperature variable. Estimates of mean annual flow (MAF) adjusted to non-reference gages (Falcone, 2011; McKay *et al.*, 2012) were obtained from the NHDPlusv2 dataset ([www.epa.gov/waterdata/nhdplus-national-hydrography-dataset-plus](http://www.epa.gov/waterdata/nhdplus-national-hydrography-dataset-plus)). Occurrence data collected at 489 unique sites covering 10 western states (Figure 4-2) was used to develop both sets of species distribution models (SDMs) described below (Figure 4-1).

#### 4.2.1 Models for assessing regional climate vulnerability

We developed *range-wide SDMs* to associate the occurrence of rainbow and cutthroat trout with a set of basic natural environmental variables previously found to be important predictors of suitable habitat (Wenger *et al.*, 2011). We modeled species occurrence as a logistic function of mean August stream temperature, mean annual flow, and reach slope using boosted

regression trees (BRTs). BRTs can accommodate a variety of data types and distributions, fit nonlinear responses and interactions and are consistently among the top performing methods for distribution modeling (Elith, Leathwick & Hastie, 2008). BRTs consist of a large number of simple classification trees fit in sequence to explain residual variation not fit by preceding trees (see (Elith, Leathwick & Hastie, 2008) for a thorough explanation of BRTs). We parameterized BRTs using guidance from the literature (Elith, Leathwick & Hastie, 2008) and assessed their out-of-sample performance using tenfold cross validation repeated five times (Leathwick *et al.*, 2006). We used area under the receiver operating characteristic curve (AUC) as a measure of a model's ability to discriminate between presence and absence (Pearce & Ferrier, 2000). Adequate discrimination is often defined for  $AUC \geq 0.7$  (Homer & Lemeshow, 2000); however, we broadened our criteria for acceptable performance to 0.65 given the rigor of our repeat measure of out-of-sample performance (Kohavi, 1995). Estimates of within-model fit (i.e. performance on training data) are misleadingly high and inappropriate for BRTs (Elith, Leathwick & Hastie, 2008) and are not provided here.



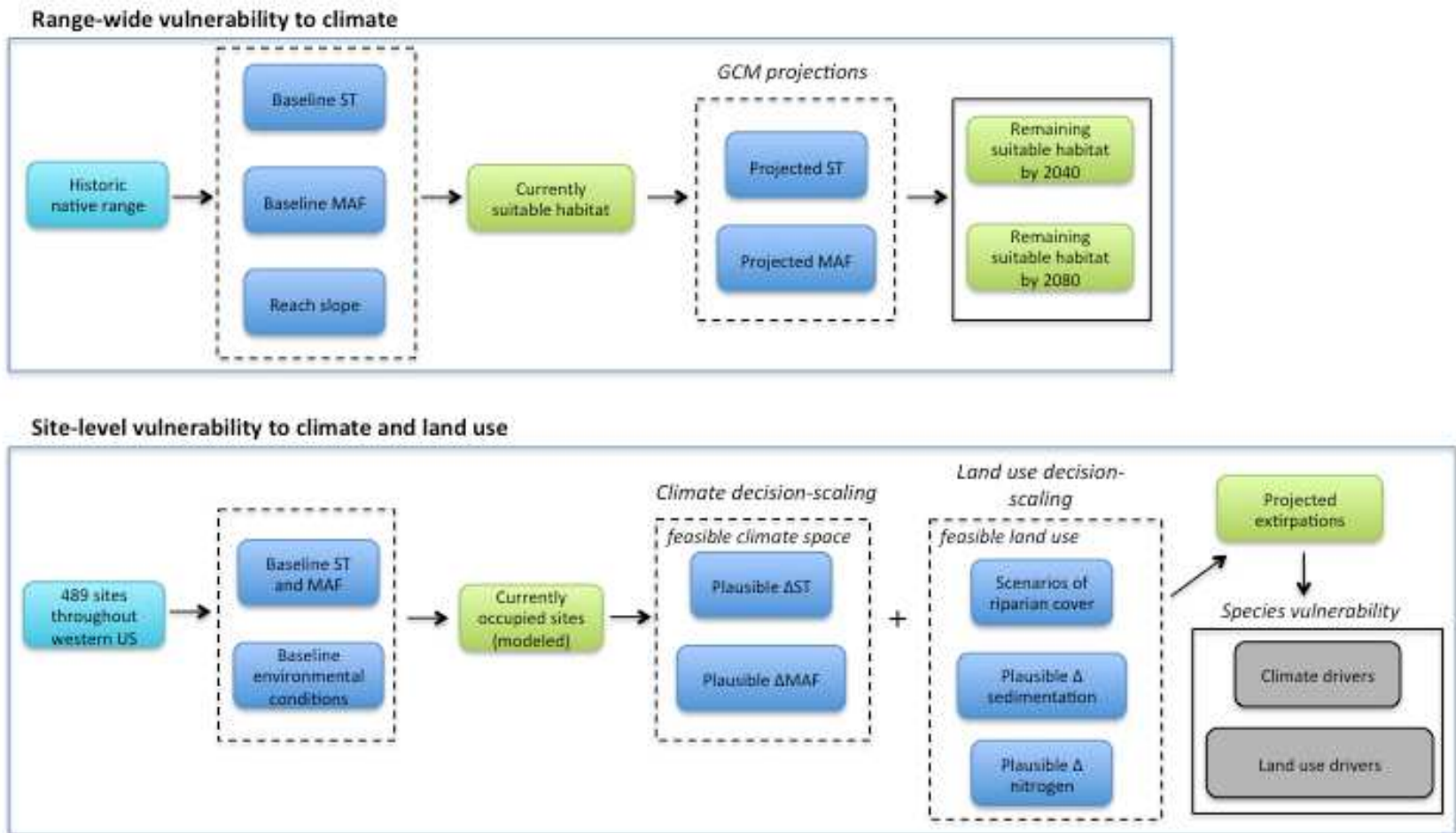


Figure 4-1. Approaches employed in this analysis to assess range-wide and site-level vulnerability of rainbow trout and cutthroat trout to components of global change. Under the range-wide approach, projected changes in stream temperature and mean annual flow for the A1B scenario are incorporated into the range-wide species distribution models (SDMs). Climate projections are used to assess future changes to suitable habitat occurring throughout species' ranges. Recognizing that climate projections are uncertain, we broadly define feasible climate space to encompass diverse climate futures as part of the site-level assessment. We consider alternative scenarios for additional non-climatic factors to investigate how local conditions affected by land use may shape species' vulnerability using the set of *local SDMs*. Projected climate data were obtained from the USFS Rocky Mountain Research Station through the NorWeST and Western U.S. Streamflow Metric project portals. ST = stream temperature; MAF = Mean Annual Flow.

We gained insight from our BRT models using two key measures for interpretation. These included: (1) relative influence, a measure ranging between 0 and 100% that describes the contribution of each predictor to the final model, and (2) partial dependence plots that visualize how the dependence of the response variable change across a gradient of values for an individual predictor. Measures of relative influence are non-parametric and convey the relative contributions of predictors to a BRT model, offering a method for interpreting their importance.

To enable consistent mapping across geographic ranges, we attributed NHDPlusv2 stream reaches with baseline stream temperatures (1993-2011) and flows (1977-2006). The baseline period for stream temperature covers the timeframe for which a majority of historic data records are available. Estimates of future stream temperature and flow were derived from climate projections for 2030-2059 and 2070-2099 (hereafter referred to as 2040 and 2080, respectively) using an ensemble mean of 10 climate models under the midrange A1B scenario. The A1B scenario (CMIP3) describes a future marked by rapid economic growth, low population growth and implementation of efficient technology and is most similar to the CMIP5 RCP 6.0 trajectory (Walsh *et al.*, 2014). Data for baseline and projected stream temperature and flow were compiled from the Rocky Mountain Research Station through the NorWeST (stream temperature) and Western U.S. Streamflow Metric efforts (<http://www.fs.fed.us/rm/boise/AWAE/projects/>). NorWeST future stream temperature estimates were derived from down-scaled air temperature projections and account for differential air-stream sensitivities that exist among basins. Methods for streamflow projections are described fully in Wenger *et al.* (2010). Briefly, the Variable Infiltration Capacity (VIC) model was used to simulate runoff at a daily time step at a resolution of 1/16° and flows were routed downstream using the NHDPlusv2 dataset.

Validated BRT models were then applied to predict species distribution under baseline and future conditions across all stream reaches within respective geographic domains. Using species prevalence (i.e. the proportion of survey sites where a species was detected) as the classification threshold (Liu *et al.*, 2005), we converted continuous values of predicted probability of occurrence into presence/absence for each stream reach. Rainbow trout and cutthroat trout have colonized suitable habitats over millennia and are widely distributed across basic environmental gradients (Behnke, 2010; Isaak *et al.*, 2015). We therefore used predictions of currently suitable habitat within species' native ranges as our basis for assessing vulnerability, specifically by estimating the proportion of suitable habitat projected to remain under future scenarios. Because estimates of habitat loss based on stream length do not account for variation in stream size, we quantified volumetric habitat loss using mean annual flow as a surrogate for stream size (Ruesch *et al.*, 2012).

Changes in configuration of habitat are likely to intensify additional climate change impacts (Roberts *et al.*, 2013). To assess how projected changes in suitable habitat will influence fragment size, we quantified habitat fragmentation using measures of contiguous suitable stream length for the three time periods. We recognize range expansion as a potential species response to climate change (Parmesan, 2006) but did not consider it in this analysis because proper assessment requires information on species' dispersal abilities and the rate of climate velocity (Isaak *et al.*, 2016) as well as information on habitat connectivity (Jaeger, Olden & Pelland, 2014) and movement barriers (Januchowski-Hartley *et al.*, 2013).

#### 4.2.2 Models for assessing local vulnerability to climate and anthropogenic stressors

We fit an additional set of SDMs (hereafter referred to as *local SDMs*) to investigate how additional environmental variables will shape species' vulnerability across the 489 widely distributed sites (Figure 4-2). For predictor variables we incorporated stream survey data on

sedimentation and riparian cover, important components of stream habitat for trout (Muhlfeld *et al.*, 2015), in addition to stream temperature and streamflow variables described above.

Additional predictor variables included cumulative nitrogen inputs and a baseflow index (Table A2 - 1). We developed *local SDMs* for rainbow trout and cutthroat trout using the BRT parameterization and cross-validation procedures described in the preceding section for *range-wide SDMs*.

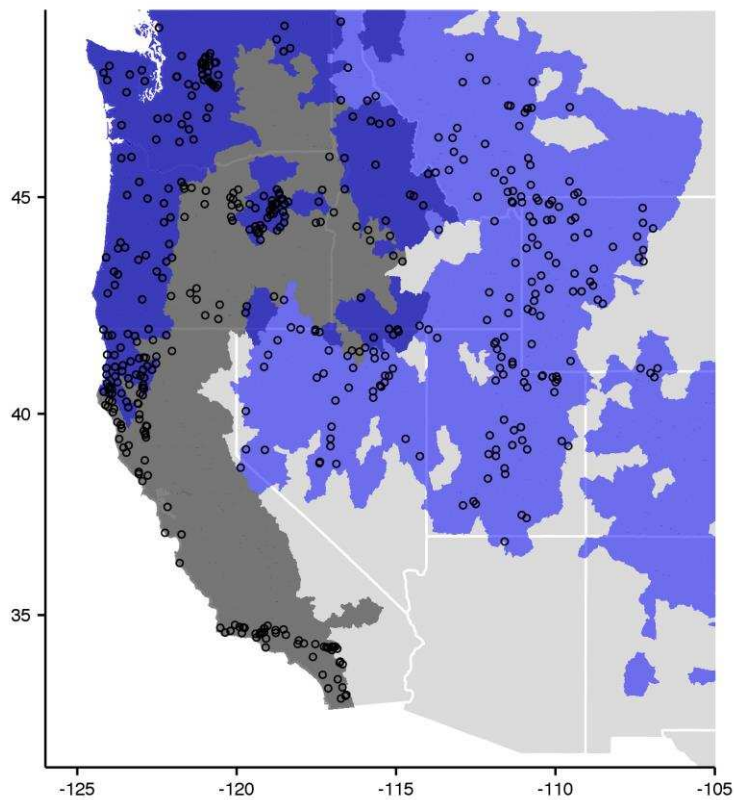


Figure 4-2. Fish survey locations (n = 489) within historic native geographic ranges of cutthroat trout (light blue) and rainbow trout (dark grey). Historic range overlap is shown in dark blue. Occurrence data used in this analysis originated from regional and national stream surveys conducted by the U.S. EPA.

#### 4.2.3 Vulnerability to changes in climate and land use using decision scaling

Concurrent changes in land use and climate necessitate that efforts to assess vulnerability to global change consider both dimensions simultaneously (Penaluna *et al.*, 2015). Here we considered plausible scenarios to evaluate how climate-driven effects could interact with

additional environmental changes to influence the vulnerability of trout species. Recognizing the diverse ways in which global change will manifest in stream ecosystems, we developed a suite of scenario-based analyses to investigate potential futures. For one set of analyses, we focused on stream temperature and assessed interactions with major land use influences. In a second set of analyses, we considered a more comprehensive feasible climate space defined by streamflow in addition to stream temperature and investigated potential climate adaptation benefits of riparian management. With these analyses, we aimed to explore the vulnerability of fish species to future climate in a way that could proceed largely independently of climate models and would also allow us to explore potential impacts over a broad range of climate and land use futures. In particular, we were interested in identifying primary environmental influences on species vulnerability including potential thresholds and interactions involving climate and land use parameters. Such information could be considered “decision relevant” for its salience to risk management (Weaver *et al.*, 2013).

We elected to use a “decision scaling” approach that has emerged to address issues of climate uncertainty primarily in the field of water resources management (Brown *et al.*, 2012). In contrast to the traditional top-down approach where climate projections from general circulation models (GCM) are used to infer vulnerability, decision scaling occurs in inverse fashion. Decision scaling begins by defining vulnerable ranges for a decision variable (e.g. ranges could be probability of occurrence for a fish species), and then proceeds by evaluating which combinations of climate and other parameters lead to vulnerable outcomes. As an additional step, incorporation of climate projections is used to evaluate plausibility of modeled vulnerabilities (Singh *et al.*, 2014).

#### 4.2.4 Stream temperature

We defined one dimension of feasible climate space for our decision scaling approach using future mean August stream temperatures that would arise due to potential increases of 0-4 °C above baseline values (1993-2011). Although widespread stream temperature increases of 4 °C are unlikely throughout the western United States, our intent was to bracket the range of possibilities from no to extreme change with our scenarios. We computed the probability of occurrence for each species at all sites by incrementally adjusting baseline temperatures using 0.25° increments to encompass the range of feasible temperature increases from 0° to 4°. We assessed the plausibility of future stream temperature warming under the A1B scenario for the 2040s (2031-2060) and 2080s (2061-2100) using the NorWest stream temperature data projected from a ten model ensemble selected to best simulate historic temperatures (Isaak *et al.*, 2015). Plausible temperature increases were defined as the range of stream temperature warming projected to occur among currently suitable streams within each species' geographic range.

#### 4.2.5 Streamflow

In addition to stream temperature, we considered potential changes in streamflow as the second dimension of feasible climate space within our decision scaling analysis. Climate change projections are less certain for surface hydroclimatology, with model disagreement on the directionality of change in runoff (Milly, Dunne & Vecchia, 2005). A recent study by Seager *et al.* (2012), however, examined changes in runoff by 2040 and found largely consistent decreases in annual average runoff of approximately 10% for major basins in the southwest, but with substantial spatial variability throughout the western United States (16 CMIP5 models, RCP8.5). We therefore developed scenarios that were intended to bracket a wide range of potential future streamflows, but focused primarily on decreased streamflow. We derived estimates of historic streamflow from the NHDPlus dataset (<http://www.epa.gov/waterdata/nhdplus-national->

hydrography-dataset-plus) and altered these to depict MAFs that would result from decreases in historical flows ranging between -5% and -25% using 5% increments. We also considered potential increases in MAF of +5% and +10%. As an alternative to MAF, we investigated mean annual runoff (MAR), a metric that standardizes flows by drainage area (Poff, Bledsoe & Cuhaciyan, 2006; Poff *et al.*, 2010) to represent streamflow permanence/stream size, but ultimately selected MAF because it was found to have greater relative influence in SDMs of rainbow and cutthroat trout (Harrison-Atlas, unpublished data).

#### 4.2.6 Land use

Previous research on anthropogenic drivers of fish distribution found sedimentation and nitrogen to be primary drivers (Harrison-Atlas, Poff & Theobald, In prep.) whose proximate causes include agricultural and urban land uses (Allan, 2004). Although sedimentation is known to affect stream condition via a unique pathway, findings from recent experimental studies suggest that negative impacts of sedimentation on stream biota may be amplified at higher stream temperatures (Piggott *et al.*, 2012). Here we focused exclusively on stream temperature warming as the climate driver and examined how vulnerability is affected across continuous gradients of nitrogen and sedimentation reflecting potential land use scenarios.

##### 4.2.6.1 Sedimentation

Salmonids are particularly sensitive to fine sediments that can impact respiratory surfaces and degrade spawning habitat by embedding substrate needed for recruitment (Bjornn & Reiser, 1991; Kemp *et al.*, 2011). Embeddedness varies across natural geologic gradients (Potyondy, 1993) but also responds to activities that reduce bank stability and increase sedimentation (Nerbonne & Vondracek, 2001; Poff, Bledsoe & Cuhaciyan, 2006). In a national effort to assess watershed vulnerability to climate change, the U.S. Forest Service considered embeddedness to be a key indicator of sensitivity through its association with habitat quality for salmonids

(Furniss *et al.*, 2013). We determined embeddedness to be a reliable metric (see A.2. for more information) and adopted it as a surrogate for sedimentation.

#### *4.2.6.2 Nitrogen*

Nutrient levels in streams are affected by agricultural and urban land uses through application of fertilizer and animal waste and through soil erosion (Allan & Castillo, 2007). In addition, nitrogen may enter the stream through atmospheric deposition. We focused on nitrogen as a key nutrient due to its significance in explaining contemporary cold-water fish distributions as well as its established linkages with land use (Harrison-Atlas, Poff & Theobald, In prep.). We quantified current levels of cumulative nitrogen inputs by accounting for atmospheric and terrestrial sources upstream of each study site. Methods are described in A.2. Supporting Information.

#### *4.2.6.3 Feasible scenarios for sedimentation and nitrogen*

We defined a broad range of feasible space to reflect in-stream conditions that would arise from either dramatic intensification of land use activities or, conversely, marked reduction in the magnitude of nitrogen and sediment delivery to streams (i.e. through implementation of conservation measures). Therefore, we considered feasible land use scenarios to be those that encompassed potentially large increases in nitrogen and sedimentation upwards of 100% over baseline levels as well as reductions upwards of 50% from baseline levels. We implemented these scenarios by incrementally adjusting baseline values using 5% increments. We capped resulting sedimentation values so as not to exceed a maximum potential value of 100% embedded.

#### *4.2.7 Riparian vegetation for climate adaptation*

Riparian vegetation provides critical ecological functions that include temperature regulation through shading, control of sediment delivery, buffering of nutrient inflows, support



of terrestrial invertebrate food base and maintenance of in-stream habitat (Gregory *et al.*, 1991; Naiman & Decamps, 1997). Owing to these benefits, augmentation of riparian vegetation is commonly utilized for river restoration in the United States (Bernhardt *et al.*, 2005). In addition, riparian improvements are increasingly highlighted in the realm of climate adaptation as an effective strategy for coping with anticipated exposure to warming and other climatic changes (Palmer *et al.*, 2008; Lawler, 2009; Seavy *et al.*, 2009; Capon *et al.*, 2013). To explore the significance of riparian vegetation for climate change vulnerability we considered three scenarios. The scenarios consisted of: 1) a preservation scenario in which current riparian cover is assumed to persist into the future (i.e. 2080); 2) a loss scenario in which riparian cover is reduced by 25%; and 3) an adaptation scenario in which riparian cover is preemptively increased by 25% (Mantyka-Pringle *et al.*, 2014). Increases in riparian cover were capped for the adaptation scenario so as not to exceed the maximum potential riparian cover. We focused on cutthroat trout for this analysis due to their presumed high sensitivity to warming.

#### 4.2.8 *Quantifying species vulnerability to climate and anthropogenic drivers*

For the climate adaptation analysis involving riparian vegetation, we defined plausible scenarios of future climate within our feasible climate space using all pairwise combinations of potential changes in ST and MAF (Pyne & Poff, 2016). We implemented riparian cover scenarios as an additional modifier by superimposing changes in riparian cover onto feasible climate space. In other words, we conducted three decision scaling analyses using the same feasible climate space but differing in the amount of riparian vegetation. For all other analyses, we defined feasible space using all pairwise combinations of potential changes in ST and the respective land use variable. We focused on ST as the climate variable because future warming is more certain than changes in hydrology. As a first order approximation, we assumed that climate and land use scenarios were equally probable for all sites (i.e. climate space is uniformly

plausible across the study area). Thus we implemented all feasible environmental changes by incrementing values at each site relative to baseline conditions.

Using the *local SDMs*, we computed for each site the probability of species occurrence under each incremental climate and land use realization within feasible climate space. Following guidance from Liu *et al.* (2005), we transformed modeled species occurrence probabilities into presences/absences using species prevalence (proportion of species occurrence among sampled sites) as the conversion threshold. We quantified vulnerability throughout feasible climate space as the proportion of sites where a species was a) predicted to be present under baseline climate conditions for each land use scenario and b) projected to become extirpated. We present the results of our decision-scaling analysis using a “heat map” approach (Poff *et al.*, 2015) to visually depict vulnerability in relation to potential environmental changes. The heat map shows variation in projected vulnerability within feasible climate-land use space. All analyses were performed using R version 3.3.0. BRTs were parameterized using caret package version 6.0-68 and fit using gbm package version 2.1.1. Spatial analyses were performed in ArcGIS 10 (ESRI, Redlands, CA, USA).

### **4.3. Results**

Future warming of August stream temperatures relative to baseline conditions is likely for nearly all streams in our study area with the exception of coastal California. The magnitude of projected stream temperature warming is greatest in the Columbia basin of the Pacific Northwest and large portions of the Colorado River basin (Figure A3 - 3). Among currently suitable reaches for cutthroat trout, mean increases of  $1.2 \pm 0.3^{\circ}\text{C}$  are projected by 2040 with greater magnitude of warming ( $2.0 \pm 0.5^{\circ}\text{C}$ ) projected by 2080. The magnitude of projected warming is similar for rainbow trout ( $1.2 \pm 0.4^{\circ}\text{C}$  by 2040;  $2.0 \pm 0.7^{\circ}\text{C}$  by 2080; Figure A3 - 5).

For 2080, decreases in MAF are projected for much of the western United States with the greatest reductions occurring throughout the southwest (Figure A3 - 4). Increases in MAF are projected for much of the Columbia basin. More localized variation in projected changes in MAF is evident within major basins (Figure A3 - 6).

#### 4.3.1 Results for species distribution models

Both sets of BRT models (*range-wide* and *local SDMs*) had acceptable performance with AUC values ranging between 0.67-0.81 (Table 4-2). Additional measures of performance and details of model parameterization are provided in Table A3 - 4. Measures of relative influence indicated that MAF and ST were among the most important variables for cutthroat trout under both sets of models. In order of descending importance, influential variables in the *local SDM* for cutthroat trout were MAF, baseflow, ST, nitrogen, embeddedness, and riparian cover. ST and MAF were the two most influential variables in the *range-wide SDM* for rainbow trout with reach slope accounting for the remaining 18% of variable importance. For the rainbow trout *local SDM*, ST, nitrogen, embeddedness, and MAF comprised greater than 81% of total variable importance with riparian cover and baseflow accounting for 10% and 8% of model outcomes, respectively.

Table 4-2. Species distribution models for assessing range-wide climate-induced vulnerability and local vulnerability to climate and land use scenarios. Cross-validated performance measures were obtained using withheld subsets of occurrence data. The significance of boosted regression tree model parameters is described in (Elith, Leathwick & Hastie, 2008). AUC = area under the receiver operating characteristic curve, MAF = mean annual flow, ST = stream temperature, RC = riparian cover; SED = embeddedness; N = nitrogen; BFI = base flow index.

Species	Model	Variables and relative influence	AUC
Cutthroat trout	Range-wide	MAF (54.2%); ST (40.8%); Slope (5.0%)	0.67
	Local	MAF (19.3%); BFI (19.1%); ST (18.6%); N (18.1%); SED (13.9%); RC (11.03%)	0.71
Rainbow trout	Range-wide	ST (53.7%); MAF (28.1%); Slope (18.2%)	0.76
	Local	ST (28.0%); N (23.0%); SED (15.3%); MAF (15.1%); RC (10.3%); BFI (8.3%)	0.81

### 4.3.2 Range-wide climate vulnerability

We projected greater range-wide vulnerability for cutthroat trout than for rainbow trout. Losses of suitable habitat by length were upwards of 34% for cutthroat trout by 2080 (Table 4-3). In contrast, we projected relatively modest losses for rainbow trout by 2080, with the length of suitable habitat decreasing by 14%. For both species habitat losses by volume exceeded those quantified using stream length (Figure 4-3). For example, suitable habitat volume for rainbow trout is projected to decline upwards of 31% by 2080, which exceeds length-based estimates of habitat loss by 137%. At a regional extent, habitat loss for cutthroat trout is most evident along the Cascade Range in the Pacific Northwest as well as in portions of Idaho and western Montana (Figure 4-4; Figure A3 - 7). Projected habitat loss for rainbow trout appears subtle at a regional extent, but exhibits finer-scale variability (Figure 4-5). For example, habitat loss for rainbow trout is substantial throughout portions of central Oregon and Washington (Figure A3 - 8) that are projected to experience high magnitude of stream temperature warming (Figure A3 - 3).

Table 4-3. Current and projected length (km) of suitable habitat for cutthroat trout and rainbow trout remaining within species' respective geographic ranges by 2040 and 2080. Stream temperature and streamflow were projected using an ensemble modeling approach under the A1B scenario.

<b>Species</b>	<b>Baseline</b>	<b>2040</b>	<b>2080</b>
Cutthroat trout	109,729	86,989	71,228
Rainbow trout	179,740	168,444	155,276

Projected ST warming was the predominant driver of habitat loss as compared to MAF (see A.3.). Examination of the spatial patterning of habitat loss reveals that vulnerability varies along an elevational gradient. Loss of thermally suitable habitat generally progresses in the upstream direction as effects of warming expand to higher elevation streams over time (Figure A3 - 9). This pattern of loss effectively fragments remaining habitat, further restricting cutthroat trout to isolated headwater stream networks (Figure 4-4D). By 2080 we project that mean fragment length will decrease by approximately 29% (Table A3 - 5).

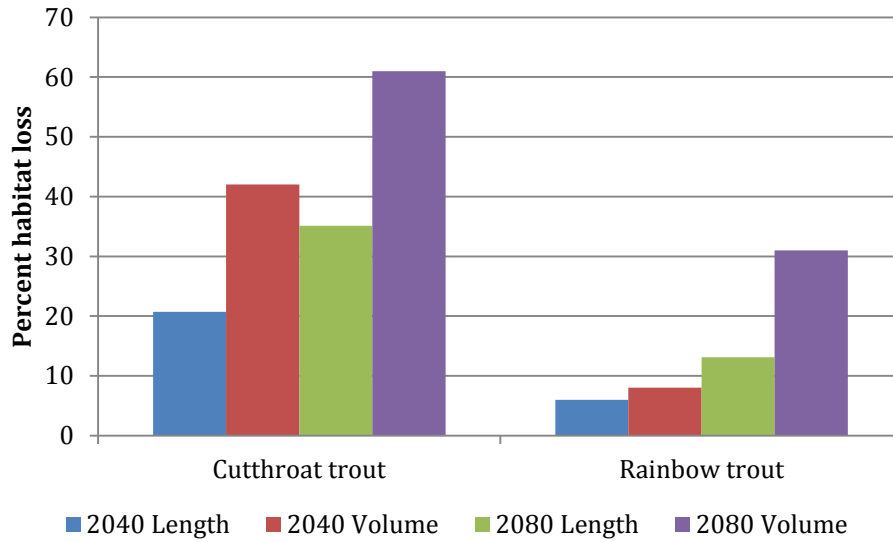


Figure 4-3. Projected loss of suitable habitat for cutthroat trout and rainbow trout as estimated by stream length and volume. Habitat loss is quantified relative to baseline habitat within each species' geographic range and describes the proportion of currently suitable habitat projected to become unsuitable by 2040 and 2080. Ensemble-based projections for August stream temperature and mean annual flow for the A1B scenario were acquired from the US Forest Service's NorWeST (<http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html>) and Western U.S. Streamflow Metrics ([http://www.fs.fed.us/rm/boise/AWAE/projects/modeled\\_stream\\_flow\\_metrics.shtml](http://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml)) projects.

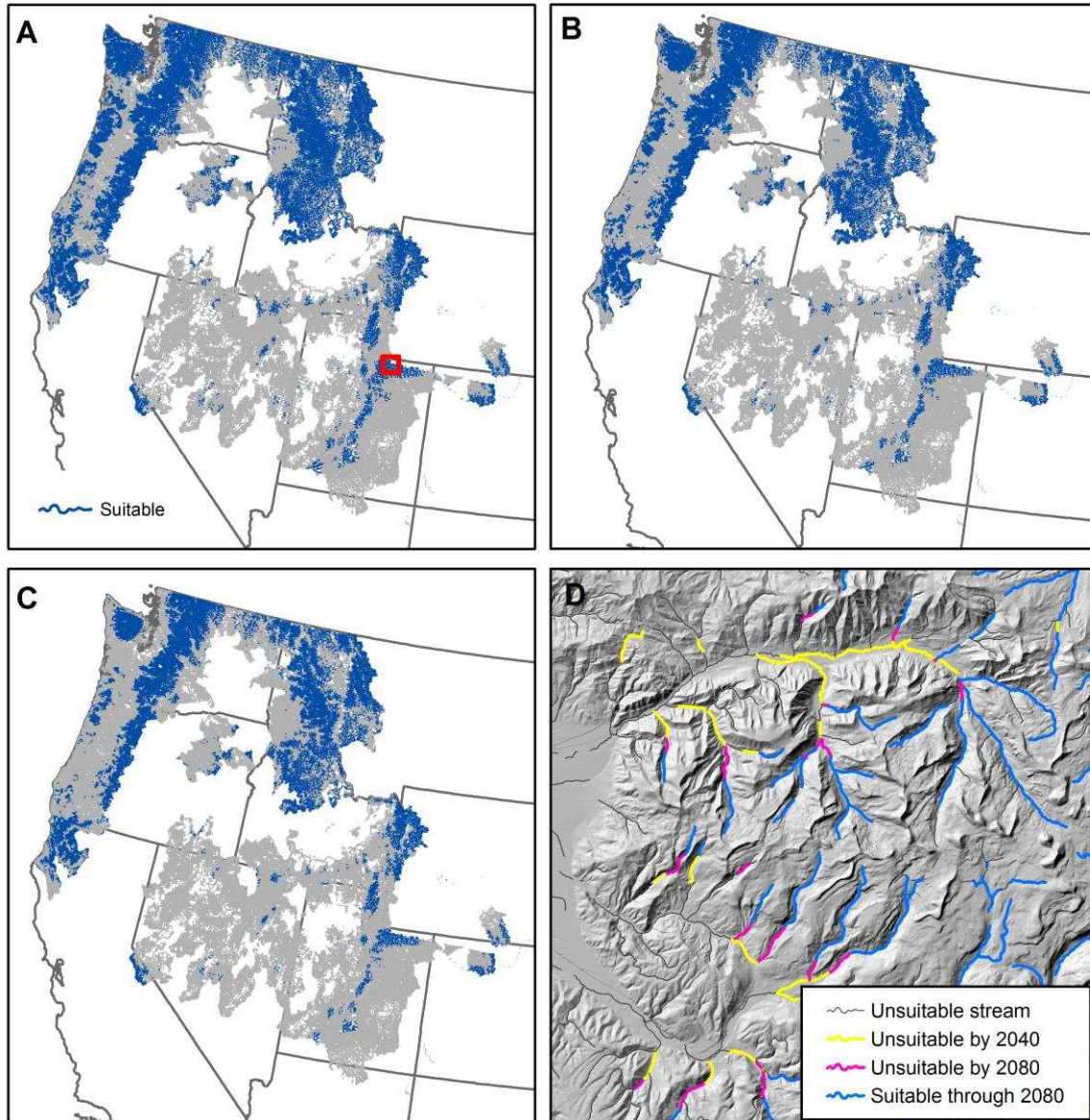


Figure 4-4. Suitable stream habitat for cutthroat trout under baseline climate scenario (109,729 km; A) and remaining suitable habitat under projected stream temperature and flow for 2040 (86,989 km; B) and 2080 (71,228 km; C). Upstream progression of habitat loss is evident at fine-scales against the backdrop of a terrain hillshade (USGS; D), isolating remaining habitat through fragmentation of headwater streams. Extent of the inset map (D) is identified by the bounding box in A.

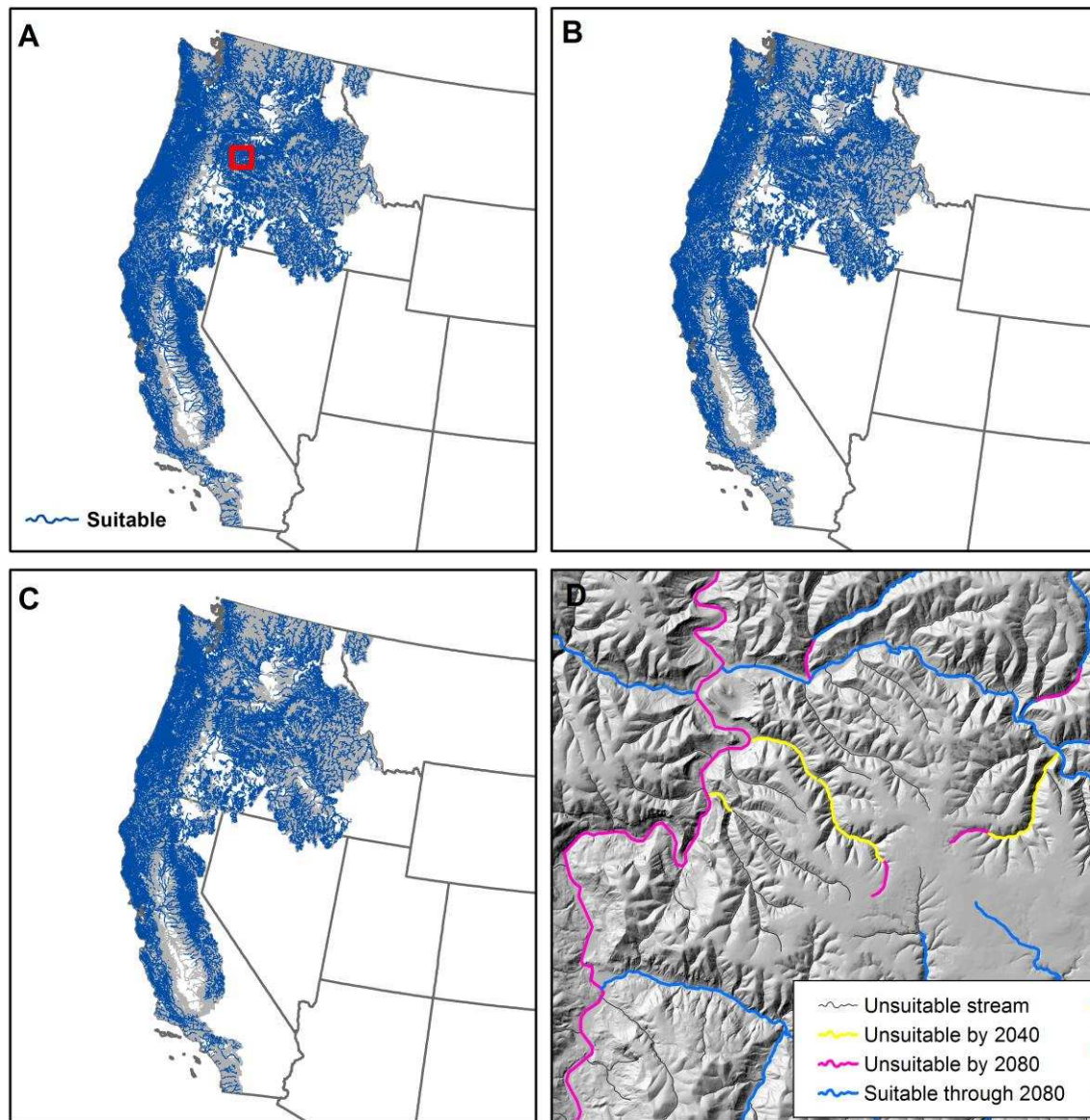


Figure 4-5. Suitable stream habitat for rainbow trout under baseline climate scenario (179,740 km; A) and remaining suitable habitat under projected stream temperature and streamflow for 2040 (168,444 km; B) and 2080 (155,276 km; C). Range wide reductions in suitable habitat exceed 13% by 2080 but appear modest at broad spatial extent. The spatial patterning of habitat loss is apparent at local scales (D), with some mainstem rivers (John Day River shown here) and currently marginal streams becoming unsuitable due to warming.

#### 4.3.3 Site-level vulnerability to changes in climate and land use

Land use influences were found to be predominant contributors to species vulnerability as both independent drivers and interactive stressors alongside stream temperature warming. We characterized important differences in species vulnerability across feasible climate-land use

space. Similar to our range-wide assessment, we found that cutthroat trout were more sensitive to warming than rainbow trout. Vulnerability of cutthroat trout to warming was exacerbated by increased sedimentation with extirpations approaching 80% of currently occupied sites (Figure 4-6). The heat map for nitrogen revealed a more complex interaction for cutthroat trout. For example, the highest vulnerabilities occurred in response to moderate to extreme warming and were most severe for changes in nitrogen within 25% of baseline levels (Figure 4-7).

In contrast, vulnerability of rainbow trout was driven primarily by land use influences as opposed to independent effects of stream temperature warming. A threshold-like response of rainbow trout vulnerability to sedimentation was apparent for increases in sedimentation that exceeded baseline levels by approximately 70% (Figure 4-8). Interactions between stream temperature and sedimentation elevated vulnerability of rainbow trout to warming.

Vulnerabilities were greatest in cases where moderate to extreme stream temperature warming coincided with large (> 70%) increases in sedimentation. We found a strong, negative reaction to increasing nitrogen levels for rainbow trout such that apparent responses to warming were minimal in comparison to detrimental effects of increased nitrogen (Figure 4-9). For example, maximum warming-induced vulnerability of rainbow trout was found to be less than 10% as compared to maximum nitrogen-induced vulnerability that approached 100% extirpation.



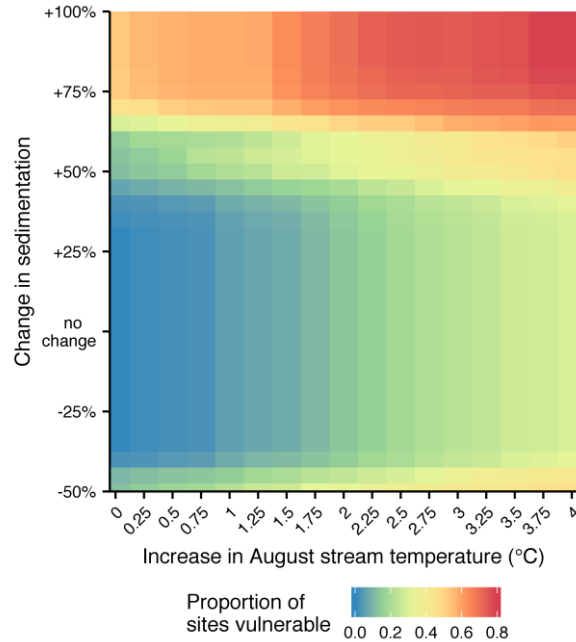


Figure 4-6. Decision-scaling heat map for vulnerability of cutthroat trout to plausible changes in stream temperature and sedimentation. Vulnerability is defined for each increment within feasible space as the proportion of survey sites where cutthroat trout are predicted to be present under the null scenario and are projected to become extirpated. The color ramp is scaled to reflect the maximum vulnerability projected within this feasible climate-land use space. Climate and sedimentation scenarios are applied to all study sites with uniform probability.

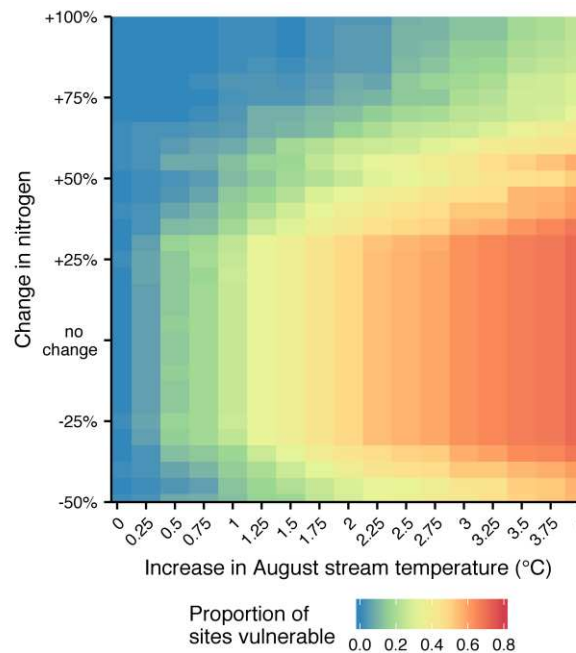


Figure 4-7. Decision-scaling heat map for vulnerability of cutthroat trout to plausible changes in stream temperature and nitrogen. Vulnerability is defined for each increment within feasible space as the proportion of survey sites where cutthroat trout are predicted to be present under the null scenario and are projected to become extirpated. The color ramp is scaled to reflect the maximum vulnerability projected within this feasible climate-land use space. Climate and nitrogen scenarios are applied to all study sites with uniform probability.

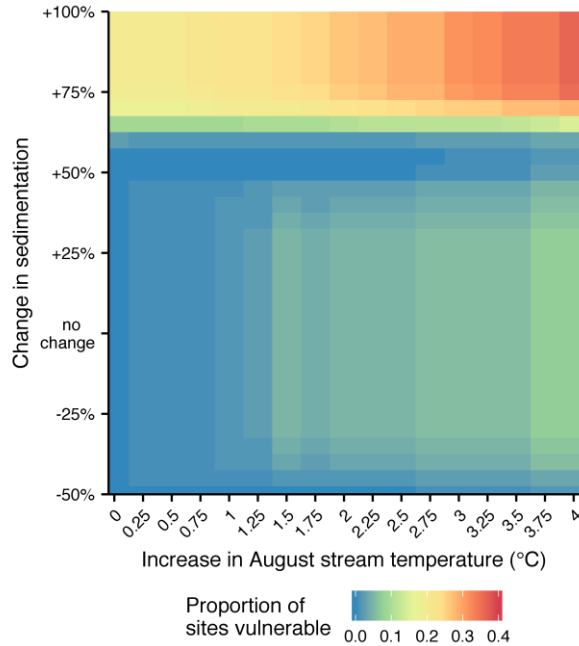


Figure 4-8. Decision-scaling heat map for vulnerability of rainbow trout to plausible changes in stream temperature and sedimentation. Vulnerability is defined for each increment within feasible space as the proportion of survey sites where rainbow trout are predicted to be present under the null scenario and are projected to become extirpated. The color ramp is scaled to reflect the maximum vulnerability projected within this feasible climate-land use space. Climate and sedimentation scenarios are applied to all study sites with uniform probability.

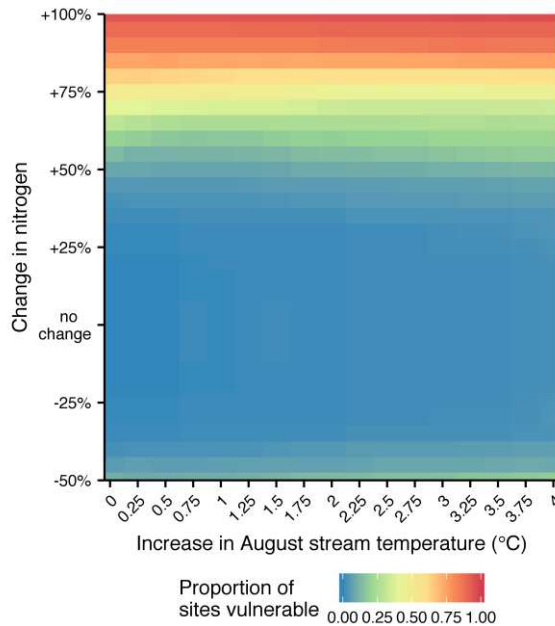


Figure 4-9. Decision-scaling heat map for vulnerability of rainbow trout to plausible changes in stream temperature and sedimentation. Vulnerability is defined for each increment within feasible space as the proportion of survey sites where rainbow trout are predicted to be present under the null scenario and are projected to become extirpated. The color ramp is scaled to reflect the maximum vulnerability projected within this feasible climate-land use space. Climate and nitrogen scenarios are applied to all study sites with uniform probability.

#### *4.3.4 Influence of riparian vegetation on cutthroat trout vulnerability*

Cutthroat trout vulnerability to climate change differed markedly across riparian management scenarios. For instance, maximum vulnerability (i.e. the greatest proportion of sites where cutthroat trout were projected to become extirpated) increased by 19% from 0.62 in the baseline scenario (Figure 4-10B) to 0.74 under the riparian loss scenario (Figure 4-10C). Median vulnerability across feasible climate space increased by 18% under the riparian loss scenario (Table A3 - 6). We found that increasing riparian vegetation cover under the climate adaptation scenario (Figure 4-10A) reduced both maximum and median vulnerability by 22% compared to the baseline scenario. The effects of increased riparian cover in mitigating extirpations were greatest for large temperature increases but were found to be beneficial in reducing vulnerability throughout feasible climate space.

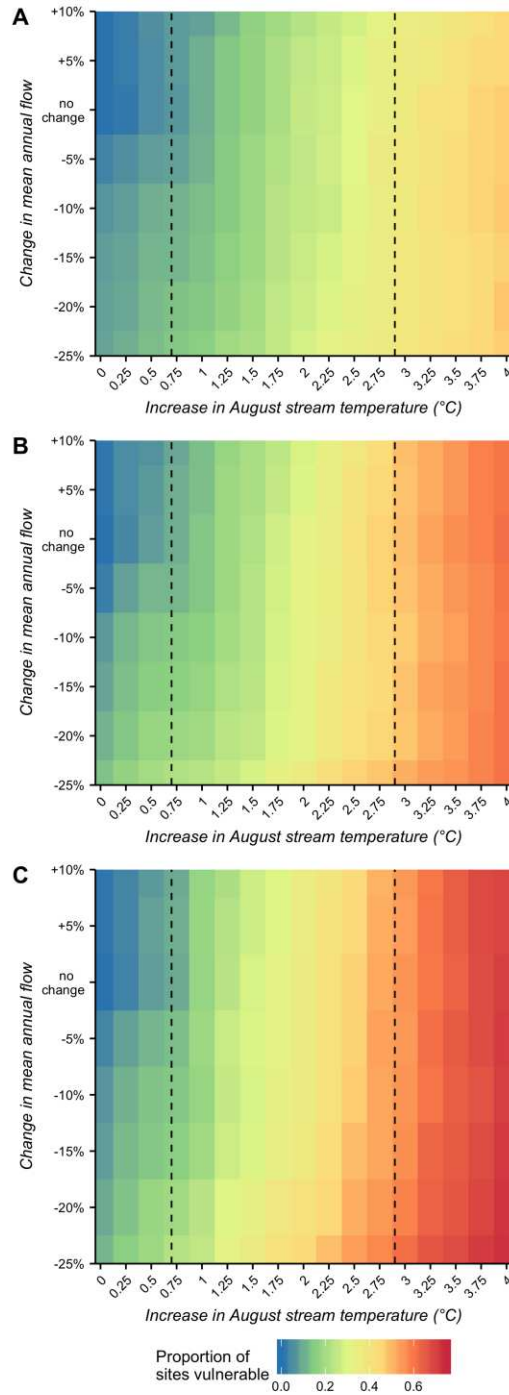


Figure 4-10. Decision-scaling heat maps for vulnerability of cutthroat trout to plausible changes in stream temperature and mean annual flow (MAF) under three alternative scenarios for riparian vegetation: A) 25% increase in riparian cover over current levels, B) maintenance of riparian cover at current levels, C) 25% reduction in riparian cover from current levels. Vulnerability is defined for each increment within feasible climate space as the proportion of survey sites where species are predicted to be present under the null scenario (baseline ST and baseline MAF) and projected to be extirpated. Vertical lines indicate the minimum and maximum stream temperature increases projected for these survey sites by 2080 under the A1B scenario (NorWeST). Climate scenarios are applied to all study sites with uniform probability.

## 4.4. Discussion

### 4.4.1 Range-wide vulnerability

Our projected habitat loss for cutthroat trout (34%) indicates substantial range-wide vulnerability resulting primarily from increased summer stream temperature. Coupled with anthropogenic activities that have historically caused widespread degradation of suitable cutthroat habitat throughout the western United States (Penaluna *et al.*, 2016) and ongoing threats from nonnative salmonids (Quist & Hubert, 2004), reductions in cutthroat trout distribution are likely to be even greater than we have quantified here. In an analysis covering interior portions of cutthroat trout's historic range, for example, Wenger *et al.* (2011) projected declines for cutthroat trout of 58% with 26% of the reductions in suitable habitat by 2080 attributable to the presence of nonnative species. Although we did not assess biotic interactions, the effects of competitive displacement by non-native brook trout (*Salvelinus fontinalis*) and rainbow trout that may benefit in some regions under climate change (Williams *et al.*, 2009) are expected to amplify range-wide vulnerability of cutthroat trout. As warming trends continue, cutthroat trout will generally be constrained to find suitable habitat at higher elevations because many populations have been restricted to headwater streams. Stream reaches that are currently too cold to support reproduction of cutthroat trout may in some cases benefit from increased temperatures (Coleman & Fausch, 2007), although concurrent expansion of competitive species into higher elevation sites may lead to further displacement of cutthroat trout (Rahel, Bierwagen & Taniguchi, 2008).

Additional environmental factors are likely to be important drivers of cutthroat trout vulnerability to climate change. For instance, in a study involving Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*), Roberts *et al.* (2013) concluded that climate-induced interactions between habitat fragmentation and stochastic disturbances pose greater threats to the

long-term persistence of high-elevation populations than do direct temperature increases. Results from our fragmentation analysis indicate that temperature driven shifts in suitable habitat will not only reduce total habitat but will also further constrain fish to shorter sections of contiguously suitable habitat. Fragmentation is likely to shape climate vulnerability in important ways. For example, fish populations restricted within fragmented habitats are more susceptible to devastating effects of disturbances that are projected to intensify under climate changes, such as wildfire (Dunham *et al.*, 2007), debris flow (Cannon *et al.*, 2010), and fluctuating stream conditions (Leppi *et al.*, 2012).

Our projected declines for rainbow trout by habitat length (14% by 2080) were modest compared to those of Wenger *et al.* (2011) who projected losses of 35% for the same time period. Two factors likely contribute to these differences. First, our use of stream temperature as opposed to air temperature is a critical distinction because the selection of temperature metric and associated methods for evaluating change due to climate forcing can lead to substantial differences in the perceived magnitude of projected warming (i.e. exposure *sensu* Glick, Stein & Edelson, 2011). As streams warm in response to increasing air temperature, at warmer temperatures they increase more slowly due to influences that include evaporative cooling and streamflow (Mohseni & Stefan, 1999). Streams additionally exhibit differential sensitivity to climate forcing with cold streams being less responsive to warming than warm streams (Luce *et al.*, 2014). Key methodological differences in Wenger *et al.* (2011) that would likely contribute to a higher magnitude of warming attributed to stream systems include the use of air temperature as a surrogate for stream temperature as well as the use of GCM air temperature deltas as an approximation of the degree of future warming (Littell *et al.*, 2011). Estimates of warming derived using this type of approach do not account for different air-stream sensitivities (i.e.

assume that magnitude of stream warming  $\sim \Delta AT$ ) and are likely to exceed estimates produced using approaches that do (Hill, Hawkins & Jin, 2014). These differences are likely to be substantial because mean air-stream sensitivities ( $\Delta ST/\Delta AT$ ) are on the order of 0.5 – 0.6 °C/°C (Hill, Hawkins & Jin, 2014; Isaak *et al.*, 2016). For example, Wenger *et al.* (2011) reported that simulations by PCM1 and MIROC3.2, the GCMs with the least and most projected warming considered in that analysis, projected mean summer air temperature increases of 2.5 °C and 5.5 °C by 2080, respectively, with the composite model falling somewhere in between (data not presented). In comparison, using NorWeST projections that account for air-stream sensitivities, we computed mean August stream temperature increases of 1.6 °C within the historic native range of rainbow trout. Differences in the degree of warming as reflected in changes in air versus stream temperature are likely to be even greater in particular regions. For example, NorWeST stream projections indicate minimal warming is likely to occur in coastal California due to oceanic buffering (Dan Isaak, personal communication).

A second difference with Wenger *et al.*'s (2011) findings is that our thermal niche characterization for rainbow trout revealed suitability to a relatively broad range of stream temperatures (i.e. sensitivity). Although methodological differences (e.g. SDM methods, use of air temperature) preclude direct comparison with the thermal niches generated in Wenger *et al.* (2011), determination of a narrower niche breadth on their part could yield higher estimates of vulnerability (Thuiller, Lavorel & Araujo, 2005; Botts *et al.*, 2013). In particular, niche differences that exist at warm temperatures are most relevant for inferring susceptibility to warming. This is because warming-induced reductions in occurrence are likely to be greater under the narrow thermal niche than for the broad thermal niche (Figure A3 - 13). Heightened sensitivity to warming that occurs under a narrow niche characterization is likely to contribute to

higher estimates of species vulnerability. Distinctive thermal niches are entirely plausible with correlative SDMs that rely on species occurrences to derive environmental relations (Elith & Leathwick, 2009). Here contrasting geographies and sampling design are important considerations given that spatial coverage and sampling of environmental gradients are known to affect niche characterization (Wiens *et al.*, 2009; Varela *et al.*, 2014). Huff *et al.* (2005) provides a clear illustration of the effect of geographic region on thermal niche estimation for rainbow trout.

Previous research on salmonids has generally found rainbow trout to be less sensitive to climate warming than other species that have lower thermal limits including bull trout (*Salvelinus confluentus*) and cutthroat trout (Rieman & McIntyre, 1993; Eaton & Scheller, 1996). Observed and projected effects of warming on rainbow trout occurrence differ by region in terms of magnitude and direction of species response. Rainbow trout distributions that are currently limited at the upstream extent of stream networks by cold temperatures may avoid net habitat loss by tracking suitable habitat in the upstream direction (Rieman & Isaak, 2010). In a study of habitat shifts due to observed warming trends in the Boise River basin of Idaho, Isaak *et al.* (2010) reported a 4% increase in suitable habitat for rainbow trout. Over the same time period, bull trout experienced an 11% reduction in suitable habitat. However, in the John Day basin in Oregon, Ruesch *et al.* (2012) projected declines in suitable stream length of 10-43% for rainbow trout by 2080, noting that volume of habitat loss would be much greater (51-87%) due to warming of currently marginal mainstem reaches. We also found that habitat losses for rainbow trout and cutthroat trout were more substantial when considered in terms of habitat volume, reflecting that warming effects on larger streams and rivers are likely to be more impactful than traditional metrics such as stream length would suggest.



Although we used mean annual flow as our streamflow metric, the addition of other biologically relevant hydrologic metrics (Poff *et al.*, 1997) would likely contribute to our understanding of how sub-annual changes to the hydrograph will influence fish species' response to climate change. In particular, changes in the timing and duration of low and high flows are likely to be ecologically important (Fausch *et al.*, 2001; Poff *et al.*, 2010). Observations of earlier snowmelt (Stewart, Cayan & Dettinger, 2005; Fritze, Stewart & Pebesma, 2011) reflect that hydrological changes are occurring in the western United States, contributing to concerns that critical low summer flows may decline along with the snowpack. Streams with reduced flow volumes may also experience increased warming (Wu *et al.*, 2012). Thus, the shrinking of available habitat and loss of refugia during summer flow periods constitute a major threat to the persistence of cold-water fishes (Isaak *et al.*, 2015). Snowmelt dominated rivers are expected to experience dramatic shifts in their hydrology, for example, with some rivers in Washington state projected to transition from snow to rain dominated flow regimes by the mid-2040s (Reidy Liermann *et al.*, 2012).

Non-climatic flow alterations may be equally profound, with widespread hydrologic alteration resulting from transformation of the natural landscape by human activities (Poff, Bledsoe & Cuhaciyan, 2006). For instance, rivers throughout arid portions of the West exhibit reduced low and high flow magnitudes due to consumptive uses (Carlisle, Wolock & Meador, 2011). The ecological significance of flow alterations (Poff & Zimmerman, 2010) that are ubiquitous suggests that flow modification will likely contribute to the vulnerability of freshwater systems to climate change. Better understanding of the anthropogenic context within which climate change impacts will be superimposed will require a thorough accounting of human influences on river systems that include existing dams, land use, invasive species and

appropriation of freshwater, and will benefit from anticipation of human responses to a changing climate (Palmer *et al.*, 2008; Olden *et al.*, 2010).

#### 4.4.2 Decision scaling

Our consideration of broadly-defined feasible climate space provided insight into a range of future vulnerabilities. This approach is in contrast to the nearly half of studies that have projected future distributions of freshwater fish species that have relied on a single GCM (Comte *et al.*, 2013). For both species we found variation in projected vulnerability across the range of feasible stream temperature warming considered. We also found major variation in projected vulnerability along the streamflow dimension of feasible climate space for the riparian adaptation scenario, although sensitivity analyses revealed that SDM projections were relatively insensitive to projected changes in MAF (see Supporting Information in A.3.). A lack of sensitivity to projected changes in MAF was also reported by Wenger *et al.* (2011). We expect that the addition of biologically relevant hydrologic indices that characterize aspects of magnitude, frequency, duration, and timing of critical flows would reveal greater sensitivity to changes in streamflow (Poff *et al.*, 1997; Olden & Poff, 2003). Given that accurate climate predictions will continue to be limited by deep uncertainties (Stainforth *et al.*, 2007) especially as they relate to future hydrology, we find considerable value in using a decision-scaling approach to explore potential outcomes as a distribution of future vulnerability.

A caveat of the decision scaling analyses is that we assumed that climate and land use scenarios were equally probable across the western US. Although we recognize that environmental changes are likely to differ in magnitude and certainty among sites, we nevertheless believe that this approach affords generalizable insights into likely drivers of species vulnerability. Future efforts may build on the analyses presented here to generate a true climate risk surface that requires integration of future climate probabilities with associated

ecological vulnerability. Although a detailed methodological description is beyond the scope of this research, such a risk assessment would entail generating regional distributions of future climate and drawing samples to characterize plausible climate vulnerabilities using a probabilistic approach.

#### *4.4.3 Site-level vulnerability to climate and land use change*

##### *4.4.3.1 Role of riparian vegetation in climate adaptation*

We uncovered important findings in climate vulnerability of cutthroat trout that were attributable to local environmental factors. For example, under a climate adaptation scenario we found that increased riparian cover shifted the distribution of vulnerability in feasible climate space towards less frequent extirpations. This finding has practical conservation implications because it suggests riparian management will convey benefits for a broad array of future climates and is likely to be an effective management tool regardless of precise climate trajectory (Wenger *et al.*, 2011). Low-risk adaptation strategies that are robust to uncertainty have been recognized as important for conservation (Lawler *et al.*, 2010) and freshwater sustainability objectives (Poff *et al.*, 2015). The role of streamside vegetation in shaping local fish response to climate change was recently investigated by Lawrence *et al.* (2014) who modeled the effects of riparian management on stream temperature. They found important benefits of riparian restoration for reducing summer stream temperatures with indirect benefits to Chinook salmon (*Oncorhynchus tshawytscha*). Cooling effects of riparian vegetation on stream temperature varied seasonally and were greatest in late summer during periods of low flow when stream temperatures are most sensitive to shading.

Widespread alteration of riparian areas by grazing and agricultural development has been attributed to increased summer stream temperatures throughout the western US (Dunham *et al.*, 1999). The length of streams in the West with moderate or high levels of riparian disturbance has

also increased in recent years (EPA, 2016), suggesting that there is both a growing need and opportunity to re-vegetate streamside areas. The potential for streamside vegetation to alleviate site-level effects of regional-scale warming is limited, however, by economic and logistical constraints associated with implementation of management actions (Bernhardt *et al.*, 2005) as well as by contextual variables such as land use, water withdrawals, and geophysical setting (e.g. stream size and channel geometry) that limit the capacity of vegetation to provide sufficient cooling (Cristea & Burges, 2009; Lawrence *et al.*, 2014). Although cooling benefits of riparian vegetation may ultimately be system specific (Li *et al.*, 1994), under a climate adaptation scenario we found that reduction in our aggregate measure of cutthroat trout vulnerability taken across 356 diverse sites was indeed substantial.

Given the broad geographic scope of our assessment as well as our aim to use reliable, previously validated stream temperature data, we did not quantify the influence of riparian vegetation on stream temperature, *per se*. Rather, our approach was to quantify the influence of riparian vegetation on fish occurrence directly. Due to their hierarchical, tree-like structure, BRTs effectively account for interactions between variables (Elith, Leathwick & Hastie, 2008). This feature gives them the ability to model for a given stream temperature differential occurrence probabilities that arise from varying proportions of riparian cover. Because our temperature metric, mean August stream temperature averages temperature variation occurring at finer temporal resolution and is representative of mean conditions at the spatial scale of a stream reach (~1 km), there are additional components of thermal suitability for which it does not account. Modeled interactions between stream temperature and riparian cover are thus likely to account for a portion of this variability because riparian vegetation exerts local influence over stream temperature (Li *et al.*, 1994). Spatial variability in stream temperature, including the

presence of microrefugia (Torgersen *et al.*, 1999), is a relevant feature of suitable habitat for cold-water fish (Baxter & Hauer, 2000; Ebersole, Liss & Frissell, 2001). The contribution of rare but important features in a riverscape to stream fish ecology is recognized as a key principle for stream fish research and management (Fausch *et al.*, 2002), in part because they can explain persistence of fish in otherwise unsuitable environments (Crozier *et al.*, 2008).

Our choice of temperature metric reflected our interest in representing particular aspects of thermal suitability. For example, mean monthly stream temperature is most relevant for assessing longer-term thermal suitability through its influence on fish growth and reproduction as opposed to acute temperature effects that result in mortality (Isaak *et al.*, 2010; Roberts *et al.*, 2013). Our vulnerability projections are therefore likely to be indicative of overall changes in suitability that arise at sub-lethal temperatures through alteration of growth rates (McCarthy *et al.*, 2009), interspecific competition, as well as through changes in incubation periods and asynchrony with prey (Dunham *et al.*, 1999; Jonsson & Jonsson, 2009; Wenger *et al.*, 2011). Though we used fish occurrence to assess climate-induced effects on fish distribution, changes in fish abundance are also likely through reductions in carrying capacity (Sloat, Osterback & Magnan, 2013). Negative relationships between trout density and warm stream temperature have previously been observed (Ebersole, Liss & Frissell, 2001; Zoellick, 2004).

#### 4.4.3.2 Land use influences on vulnerability

Freshwater systems are often subjected to multiple stressors (Dudgeon *et al.*, 2006) yet these are rarely considered alongside climate change. Using a decision-scaling approach we identified land use influences as major drivers of species vulnerability. Importantly, we found that land use may not only interact with climate warming to shape site-level extirpations, but that in some cases sedimentation and nitrogen drivers may act independently and as primary determinants of vulnerability. Collectively, these results highlight the importance of including

additional environmental factors in assessments of species vulnerability that may vary considerably due to additional, non-climatic influences. Our results also suggest that the relative influence of stressors on freshwater systems will vary according to the severity of climate change. Thus, local environmental stressors that are prominent under mild climate scenarios may be overridden in cases of extreme climate change such as with large temperature increases that exceed species' thermal tolerances. However, in situations involving strong interactions between climatic and other environmental stressors, intensification of climate may produce synergistic impacts.

A key challenge for freshwater conservation is to understand interactive effects that can arise through additive or multiplicative pathways (Olden *et al.*, 2010; Ormerod *et al.*, 2010). A number of fish studies have made progress on this front in recent years. Nelson *et al.* (2009) were among the first to forecast the cumulative effects of global change on fish species via urbanization and climate change. The two most influential pathways involved altered temperature and sedimentation – two stressors thought to affect species persistence under future scenarios of land use and climate change. In quantifying the effects of urbanization and climate change, they found the interactive effects to be greater than the sum of individual stressor effects. Mantyka-Pringle *et al.* (2014) investigated the effects of climate change and urbanization in Australia, finding that elevated nutrient loads were the main driver of fish responses. Increased stream temperature was an important driver for fish species and was found to interact with elevated nutrient loads. Although our models project heightened vulnerability for cutthroat trout and rainbow trout in response to increased sedimentation, we suspect that relevant biological mechanisms may be more in line with the concept of multiple, additive stressors as opposed to

multiplicative effects (Folt *et al.*, 1999) that have been documented in experimental studies involving stream macroinvertebrates (Piggott *et al.*, 2012; Piggott, Townsend & Matthaei, 2015).

#### **4.5. Conclusion**

Our findings collectively indicate that range-wide effects of climate change on native salmonids of the western United States will be substantial but also variable depending on the species. Cutthroat trout that have been widely extirpated throughout their native range due to habitat degradation and hybridization with rainbow trout are likely to experience further reductions in suitable habitat due in large part to their high sensitivity to warming. Conversely, we projected the widely introduced rainbow trout (Fuller, Nico & Williams, 1999) to have relatively modest vulnerability to climate change across its native geographic range. At the site level, vulnerability to land use and climatic influences revealed differential sensitivities of cutthroat trout and rainbow trout to stream warming but also implicated nutrient and sediment drivers as key determinants of fish occurrence in the future.

Our approach to assess species vulnerability to major components of global change affecting freshwater ecosystems provides insight into an array of potential ecological responses that are jointly influenced by climatic and non-climatic environmental variables. We believe that characterization of site-level vulnerability is critical to understanding of local responses that may be most relevant to managers and is complementary to range-wide assessments that are needed to provide broad overviews of species status, highlight regional trends, and to prioritize the allocation of limited conservation resources.

Ultimately, local responses to climate change will depend to a large degree on contextual environmental factors (Poff *et al.*, 2010; Rieman & Isaak, 2010; Isaak *et al.*, 2012; Penaluna *et al.*, 2015). For example, the degree of localized climate exposure may be regulated via groundwater inputs that can augment summer flows as well as by riparian shading through

moderation of stream temperature (Poole & Berman, 2001; Tague *et al.*, 2008; Lawrence *et al.*, 2014). In addition, non-climatic stressors of stream condition may further elevate the susceptibility of organisms through multiple pathways that can lead to impairment through changes in temperature and flow regimes, substrate quality, physiological growth, food availability, and biotic interactions (Nelson *et al.*, 2009; Wiley *et al.*, 2010; Wenger *et al.*, 2011; Kuemmerlen *et al.*, 2015). Furthermore, local conditions and physical features can determine the potential of species to cope with environmental changes by constraining or offering opportunities for adaptation and movement (Fausch *et al.*, 2009; Roberts *et al.*, 2013). Thus, despite the global nature of climate change, local environmental factors are likely to influence site-level responses.

Through strategic planning and application, managers can improve habitat, reduce non-climatic threats, and promote adaptive capacity to cope with the effects of climate change. Possible actions for reducing exposure to warming include maintaining the flow of groundwater to streams, restoring riparian habitat, and increasing habitat complexity and refugia by restoring channel sinuosity, undercut bank, and deep pool habitat (Hill, Hawkins & Jin, 2014; Williams *et al.*, 2015). Promotion of floodplain interactions and enhanced riparian vegetation can also provide critical hydrologic ecosystem services like sediment regulation and flood attenuation that can promote suitable habitat for salmonids. In addition, other common restoration and climate adaptations for cold-water fish species include enhancement of habitat connectivity of fragmented river and stream networks (Beechie *et al.*, 2013), restoration of impaired habitats, and removal of additional threats including invasive species (Noss, 2001; Williams *et al.*, 2015).

It has been suggested that climate adaptation has thus far been hindered by uncertainty and insufficiently precise information regarding responses of freshwater systems (Olliff *et al.*, 2016). We offer two complementary approaches for making advancements in the face of uncertainty.



First, in the preceding analysis we have outlined and followed a decision-scaling approach to vulnerability that consisted of defining feasible climate space as a function of climate-driven variables with ecological relevance; projecting vulnerability; incorporating GCM-based stream temperature projections to assess the most plausible degree of future warming; and investigating additional environmental factors that under alternative scenarios may contribute to or alleviate vulnerability. A salient feature of this approach is that it can be deployed in the absence of precise climate information to gain insight into how likely climate and land use drivers will influence ecological vulnerability (Pyne & Poff, 2016). Application of decision scaling to ecological issues is nascent, but is likely to resonate most strongly in areas related to climate adaption due to its strengths in addressing uncertainty.

Second, we believe that holistic climate adaptation strategies that target improved outcomes for native fish species and can deliver additional benefits may not only provide a good return on investment but will also likely be more suitable for implementation (Heller & Zavaleta, 2009; Wilby *et al.*, 2010). There is reason to be optimistic about the feasibility of such an approach as evidenced by the proliferation of watershed investments towards climate adaptation and mitigation (Bennett, Carroll & Hamilton, 2013). Moving forward, there is tremendous opportunity to link the management of risks relating to sedimentation and provision of water supply benefits with the safeguarding of instream flows and critical stream habitat. Finding ways to leverage diverse human interests and capital to benefit freshwater systems and the people that depend on them will be instrumental in addressing vulnerability of salmonid fish to climate change in the western US.

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## 5 Synthesis

Freshwater resources are critical to all life forms yet are changing in ways that affect human well-being and the persistence of aquatic species. In the preceding chapters I have considered a broad view of some of these issues surrounding freshwater resources that includes application of the ecosystem services framework to management contexts and the relevance of hydrologic ecosystem service (HES) studies to decision making (Chapter 2: *A systematic review of approaches to quantify hydrologic ecosystem services to inform decision making*), contemporary drivers of freshwater fish species distribution including anthropogenic disturbances (Chapter 3: *Characterizing anthropogenic and natural drivers of the occurrence of cold-water and cool-water fishes in the western United States*), and the vulnerability of freshwater fish species to climate and land use components of global change (Chapter 4: *Translating future climate exposure into range-wide and site-level vulnerability for native salmonids of the western United States*). My findings can be used to support the continued development of methods to map and quantify HES and to more tightly integrate research outputs with decision making applications, to advance the understanding of contemporary drivers of freshwater fish occurrence, and as basis for evaluating vulnerability of cold-water fish species in the western United States to climate change and other environmental stressors.

The results from the literature review conducted in Chapter 2 suggest that the field of hydrologic ecosystem services is oriented towards decision making in ways that influence the types of questions being asked, the issues that are being investigated, and the scope of analysis. Nevertheless, I discovered opportunities within the field to strengthen the application of HES science to enhance the potential impact that studies may have on decision making. Previous reviews (Seppelt *et al.*, 2011; Bagstad *et al.*, 2013a; Crossman *et al.*, 2013) have also scrutinized

the methods used to map and quantify ecosystem services, noting inconsistent application of methods among studies, and citing this finding as a major challenge for synthesizing knowledge across studies. While my findings are not in disagreement with those from other reviews, I do suggest an alternative interpretation for why there exists such variation in the application of methods and base this on evidence from my review. For example, I found compelling evidence that much of the variability in the quantification of HES can be explained by research motivations and scoping. I also found associations between HES and particular methods that are likely legacies of distinct research traditions. My findings that levels of credibility, legitimacy, and saliency tend to vary consistently among decision making contexts revealed that there are fundamental qualities of information, apart from strictly methodological considerations, that define the value of research to different applications. My findings and framework provide a basis for evaluating additional studies and can guide the design of future studies towards cultivation of robust, meaningful, and interpretable information needed for decision making (Rosenthal *et al.*, 2015). Throughout my review, I highlighted the importance of capturing the spatial dimension of hydrologic ecosystem services because of its critical role in shaping resource conflicts, distributing the flow of benefits among different groups of beneficiaries, and for influencing the geographic context behind potential management solutions.

Aspects of the framing behind the ecosystem services concept may play an important role in the safeguarding of multiple freshwater benefits including the maintenance of habitat for river and stream organisms including fish species. Faced with an uncertain future that involves changing climate, water development, and land use, the distribution of fish species will be inextricably linked to the trajectory of these pressures. My findings from Chapter 3 indicate that anthropogenic activities are important drivers of contemporary fish species distributions.



Sedimentation and nutrient enrichment were the most influential drivers on average, reflecting broad patterns of land use and human activities that have contributed to the ubiquitous transformation of the natural landscape. Although human actions will in many cases increasingly impair river and stream condition, threatening the occurrence of sensitive fishes, well planned human actions (i.e. systematic conservation planning) can also serve to mitigate extant pressures and restore habitats to more suitable conditions, prevent additional degradation from occurring, and promote the adaptation of river systems (Beechie *et al.*, 2010) and their biota to cope with impending changes in climate and land use and (Stein *et al.*, 2014).

In chapter 3, I characterized contemporary drivers of the occurrence of native cold-water and cool-water fish species of the western US. A chief objective was to establish mechanistic linkages between human activities and stream conditions that affect fish occurrence. Anthropogenic predictors were found to be influential for all species illustrating pervasive human influence in rivers and streams. My assessment of species occurrence across anthropogenic gradients revealed frequent nonlinear and threshold-like responses at varying degrees of human disturbance. This information is relevant for understanding sensitivity of species to various anthropogenic disturbances and for prescribing management actions that target appropriate disturbance pathways. My finding that summer stream temperature is a major driver of cold-water and cool-water fish occurrence is consistent with the prevailing knowledge that maximum stream temperature sets thermal limits on the distribution of these species (Rahel, 2002). However, characterization of species thermal niches revealed unique thermal optima and suitability across a gradient of stream temperature, suggesting that species may be differentially sensitive to climate warming.

In chapter 4, I expanded on my findings from chapter 3 to explore how land use in combination with climate change will likely affect the vulnerability of native salmonid fish species in the western United States. I conducted a range-wide vulnerability assessment of cutthroat trout and rainbow trout to projected changes in stream temperature and streamflow. I also used a decision scaling approach to address a recurring theme in freshwater climate change studies that implicates uncertainty and coarseness of climate projections as a hindrance towards reliable estimation of potential impacts and as a barrier to climate adaptation. Given that land use is a major driver of cold-water fish species distribution, I explored potential site-level vulnerability for a broadly defined environmental space describing both future climate and land use. Results of the range-wide analysis for cutthroat trout include considerable loss of suitable habitat, a shift in the distribution of suitable habitat towards higher elevations that retain cool stream temperatures, and likely fragmentation of thermally suitable habitat that will truncate contiguous sections of habitat. Rainbow trout are projected to have less overall climate vulnerability throughout their native range. However, losses will be substantial in areas with large magnitude of stream temperature warming and in currently marginal mainstem rivers, thereby contributing to comparatively larger declines by habitat volume. Assessment of cutthroat trout vulnerability across feasible climate space indicated that extirpations will be driven largely by changes in stream temperature rather than shifts in mean annual flow, with potentially large variation in projected extirpations depending on climate trajectory.

Scenario analyses indicate that site-level ecological responses to climate change will be predicated on and potentially overridden by additional environmental factors that include sedimentation and nitrogen. Our findings also implicate riparian vegetation as a robust strategy for coping with potential thermal impacts of climate change. Given the importance of contextual

environmental factors in shaping local responses to climate change, effective management actions to combat climate change impacts will be those that a) regulate the degree of climate exposure, for example via groundwater inputs that can augment summer flows or riparian shading that can moderate stream temperature (Poole & Berman, 2001; Tague *et al.*, 2008; Lawrence *et al.*, 2014); b) affect stream condition via non-climatic stressors that may further elevate the susceptibility of organisms through multiple pathways that can lead to impairment through changes in temperature and flow regimes, substrate quality, physiological growth, food availability, and biotic interactions (Nelson *et al.*, 2009b; Wiley *et al.*, 2010; Wenger *et al.*, 2011; Kuemmerlen *et al.*, 2015); and c) provide opportunities for adaptation and movement (Fausch *et al.*, 2009; Roberts *et al.*, 2013).

Rivers and streams are complex entities with characteristics of hierarchical systems that include scaling in time and space. Because influences of stream habitat include drivers at multiple scales (Frissell *et al.* 1986; Poff *et al.* 1997), management and conservation of freshwater systems should reflect these principles. Identification of relevant anthropogenic drivers and the pathways by which they contribute to stream degradation is a critical step in formulating effective management solutions because management actions that are not commensurate in scale with drivers are unlikely to offer sustainable solutions (Beechie *et al.* 2010). In many cases, dealing with stressors effectively will require broad-scale and systematic planning efforts, coordination across multiple entities and stakeholder groups, progressive environmental policies, and a vision for the future that balances human with environmental needs. Ecosystem services can help guide that vision, offering a framework that is capable of catering to human and environmental interests over the long term.

My research on native cold-water and cool-water fish species sheds light on critical issues surrounding contemporary drivers of occurrence and future vulnerability to climate and land use change and identifies the potential to leverage watershed investments for the dual purpose of climate adaptation. To the extent that conservation of fish and their habitat can be integrated with the management of additional ecosystem services benefits to humans, the persistence of native fish species will be aided by continued human investment in natural infrastructure and the benefits that flow from it.

## **Appendices**

### **A.1. Articles analyzed in the literature review of hydrologic ecosystem services**

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Table A1 - 1. Accompanying scores for Figure 2-3. Criteria in columns are described in Table 2-2.

<b>Motivation</b>	<b>Operational phase</b>	<b>Scenario analysis</b>	<b>Biophysical output</b>	<b>Monetary output</b>	<b>Relative ranking</b>	<b>Trade-offs</b>	<b>Model evaluation</b>	<b>Uncertainty analysis</b>	<b>Flow complexity</b>	<b>Stakeholder involvement</b>	<b>Model transparency</b>
Understanding and education	Assessment	0.08	0.88	0.12	0.12	0.40	0.48	0.16	0.40	0.12	0.65
Understanding and education	Planning	1.00	1.00	0.25	0.00	0.63	0.88	0.38	0.53	0.00	0.55
Understanding and education	Management	-	-	-	-	-	-	-	-	-	-
Cost-benefit analysis	Assessment	0.00	0.67	0.67	0.22	0.22	0.44	0.22	0.31	0.00	0.58
Cost-benefit analysis	Planning	1.00	0.69	0.92	0.08	0.23	0.46	0.31	0.48	0.08	0.53
Cost-benefit analysis	Management	1.00	1.00	0.50	0.00	0.00	0.50	1.00	0.38	0.00	0.75
Landscape management	Assessment	0.33	1.00	0.00	0.00	0.33	0.33	0.33	0.33	0.00	0.57
Landscape management	Planning	0.76	0.76	0.24	0.24	0.76	0.59	0.18	0.53	0.35	0.60
Landscape management	Management	-	-	-	-	-	-	-	-	-	-

## A.2. Supporting information for fish distribution modeling

### *Stream survey data*

Aquatic vertebrate sampling was accomplished via backpack electrofishing in third-order and smaller rivers and via raft electrofishing in ~ fourth-order and larger rivers. Wadeable streams were sampled for a length approximately 40 times the average wetted stream width. Raft sampling occurred near shore for a distance equal to 100 times the average wetted stream width of larger rivers (Whittier *et al.*, 2007). It is estimated that backpack and raft electrofishing field sampling methods used as part of the WEMAP survey respectively capture around 90% (Reynolds *et al.*, 2003) and 95% (Hughes *et al.*, 2002) of fish species present.

Water chemistry samples were collected at each site to evaluate stream condition in terms of nutrient enrichment, acidic deposition, and the presence of other contaminants (Peck *et al.*, 2006). In addition, seven physical attributes influencing stream ecology were documented at each site (Kaufmann, 1993). Physical surveys measured stream size, channel gradient, channel substrate size and type, habitat complexity and cover, riparian vegetation cover and structure, anthropogenic alterations, and channel-riparian interaction (Kaufmann *et al.*, 1999). We used sinuosity (i.e. channel curvature) as a surrogate measure of valley confinement based on the premise that sinuosity reflects the stream's response to geomorphic factors that constrain lateral migration. In rare cases where field measures of sinuosity were unavailable, we interpreted high resolution satellite imagery and recorded for each reach (defined as the length of stream 20x bankfull width upstream and downstream of survey point) the channel length ( $L_c$ ) and valley length ( $L_v$ ), computing sinuosity ( $S$ ) as  $S = L_c/L_v$  (Rosgen, 1994). A sinuosity value of 1.0 indicates a perfectly straight stream channel, low values ( $1.0 < S \leq 1.2$ ) indicate highly confined and/or high gradient settings, moderate values ( $1.2 < S \leq 1.5$ ) reflect low confinement, and high values ( $S > 1.5$ ) are typical of low gradient, meandering streams.

### *Site selection for species distribution modeling*

We obtained a database of the historic distribution of freshwater fishes at the HUC 8 watershed level from NatureServe ([natureserve.org](http://natureserve.org)). We modeled species occurrence using subsets of WEMAP/NRSA survey sites located within polygons delineating species' historic native ranges. Thermally anomalous sites located within five kilometers downstream of dams were excluded from this analysis.

### *Cross validation*

Models were trained using 10-fold cross validation. Cross-validation proceeds as follows. First, observations are divided into 10 equally-sized folds. At each iteration, model training occurs on 9/10 of the folds. The hold-out fold is then used to evaluate model performance. This process continues until all 10 of the folds have been withheld from training and used as test cases. Overall model performance is reported as the mean AUC value for all hold-outs. We repeated the cross-validation procedure five times. The repeat-CV approach can produce more reliable estimates by reducing variance associated with a single trial of cross validation (Leathwick *et al.*, 2006).

We produced joint partial dependence plots to capture interaction effects of multiple predictors. Partial dependence was assessed using the weighted tree traversal method (Friedman, 2001). We assessed the strength of interaction for all pairwise sets of predictors in our final model using Friedman's H statistic (Leathwick *et al.*, 2006; Friedman & Popescu, 2008). H ranges between 0 and 1 with higher values corresponding to stronger interaction effects. For two variables  $x_j$  and  $x_k$ , the statistic  $H_{jk}$  corresponds to the fraction of variance of  $F_{jk}(x_j, x_k)$  not captured by the sum of  $F_j(x_j) + F_k(x_k)$  considered independently (Lampa *et al.*, 2014).

### *GIS catchment-scale disturbance variables*

*Sedimentation:* Sedimentation is notoriously difficult to quantify at basin scales (de Vente and Poesen, 2005). Sedimentation is highly sensitive to “temporal lumping” (Walling 1983), in some cases with the majority of all sediment transport driven by a singular extreme weather event (Piest, Kramer & Heinemann, 1975). In addition, sedimentation may be more difficult to predict in larger basins owing to greater storage capacity. Given these challenges, we intend this variable to represent the potential for human activities to influence water quality via sedimentation processes. To estimate erosion potential at a broad-scale, we developed a RUSLE-like model that considers land use activities, slope, soil erodibility, and rainfall-runoff erosivity as contributing factors. We considered agriculture and urban land uses as two primary drivers of erosion (Wischmeier and Smith, 1978; Jones *et al.*, 2001; Brown and Froemke, 2012). We note that this variable is intended to complement our fine-grain field data that measure related quantities (i.e. embeddedness, percent sand and fine substrate, siltation, turbidity). We used Nearing’s (1997) continuous slope method to estimate gradient influences on erosion. Slope factors range between 0.05 for slope=0; 0.98 for 5 degree slopes; and 6.1 for 20 degree slopes. We obtained information on soil erodibility from the SSURGO soils database and filled in data gaps with values from STATSGO. To capture the effects of rainfall intensity and amount of runoff on the rate of erosion, we incorporated the R-Factor into our index of erosion potential. An 800 meter resolution raster of the R-Factor for the conterminous United States was obtained from NOAA (<https://data.noaa.gov/dataset/r-factor-for-the-coterminous-united-states>). Our final index of sedimentation was a composite of all contributing factors that we produced by overlaying in GIS.

*Nutrient enrichment:* We developed a spatial allocation model to map terrestrial and atmospheric nutrient inputs. Ruddy *et al.* (2006) provided a county-level summary depicting the contribution of agricultural activities to nitrogen and phosphorus inputs. We performed spatial allocation of four nutrient input categories (farm, nonfarm, manure from confined animals, and manure from unconfined animals) using a roads-removed version of the National Land Cover Dataset (NLCD 2001, Theobald unpublished dataset) as a mask. To improve the spatial representation for agricultural commodities, we simulated farmland operations using the Farmland and Agricultural Production Simulator (FLAPS; Burdett *et al.*, 2015). For each commodity type (swine, beef, dairy, sheep), we performed 10 simulations using the estimated animal units at each point as the population and generated a kernel density surface for each simulation. We differentiated between confined and unconfined farming operations using data provided by Kellogg (2002). We then distributed the total amount of nutrient for each commodity type (using the values reported by Ruddy *et al.* (2006) at the county level) using the mean density surface as weighting.

A map of atmospheric nitrogen deposition (wet and dry) was downloaded from the National Atmospheric Deposition Program (<http://nadp.sws.uiuc.edu/committees/tdep>) and re-scaled to 270 m resolution.

*Mines:* Mines are a landscape influence that have been implicated as an important stressor to freshwater ecosystems in numerous studies (e.g. Falcone *et al.*, 2010; Esselman *et al.*, 2011; Daniel *et al.*, 2014). We obtained high resolution (30m) data on the distribution of mines for 2006 (Soulard *et al.*, 2016). We presumed that the influence of each surface mine would be proportionate to its size and represented the areal extent using its spatial footprint. We reclassified the mine raster using a value of 1 to represent pixels within a surface mine and 0 for

all other pixels. For each upstream catchment, the binary mine raster was then re-weighted using the hydrological weighting scheme to account for flowlength to the survey site and level of hydrologic activity. Our final measure of mine influence was a summary of all hydrologically-reweighted surface mine pixels within a site's upstream catchment.

*Hydrological weighting:* We used a hydrologically-active weighting scheme to account for spatial variability in the potential for an upland area to influence downstream conditions by integrating local measures of proximity to the stream network and level of hydrologic activity (Peterson *et al.*, 2010). Datasets developed by the World Wildlife Fund were used as base layers for our hydrological weighting scheme. HydroSHEDS datasets have global coverage and were produced in a consistent fashion, facilitating their use in regional-scale applications. We used the finest available resolution (15 arc seconds) of the HydroSHEDS data for flow direction and flow accumulation rasters. HydroSHEDS flow direction data derived from a hydrologically conditioned elevation dataset were used to generate a raster depicting flow length from each pixel in a catchment to its outlet. We intended our estimate of flow length to serve as a coarse measure of distance in hydrologic terms. In other words, because of our intended use we were not interested in generating precise estimates of flow length, but rather aimed to capture the proximity of land use activities on a spectrum between near and far. Flow lengths were computed in ArcMap v10. We used an inverse distance weighting (IDW) scheme (King *et al.*, 2005; Van Sickle & Johnson, 2008; Peterson *et al.*, 2010) to account for decreasing influence of landscape elements as a function of their flow distance. Flow lengths were converted to kilometers; we used the inverse of the flow length as our inverse distance weighting function (i.e.  $1/\text{flow length}$ ) (King *et al.*, 2005; Van Sickle & Johnson, 2008) and rescaled W values (see formula below) from 0-1. We log transformed the flow accumulation raster to give weight to influential

terrestrial areas whose flow accumulation values were substantially lower than stream pixels. The transformed raster was used as a proxy for hydrologic activity.

For each land use disturbance variable  $j$ , we computed the cumulative disturbance (CD) in a catchment as:

$$CD_j = \sum W_i F_i D_i$$

where  $W_i$  is a 0-1 weighting factor that represents the inverse flow length from the cell to the outlet,  $F_i$  is flow accumulation in cells, and  $D_i$  is the amount of disturbance at the cell.

Cumulative disturbance measures were normalized by drainage area to account for variation in catchment size (Esselman *et al.*, 2011).



### A.2.1. Supporting references for fish distribution modeling

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Table A2 - 1. Predictor variables used to model species occurrence including codes, units, ecological rationale and associated references, and data sources. Predictors are grouped into broad categories of natural environmental variables and anthropogenic variables that include mechanisms of ecological disturbance (following Allan, 2004). See Table 3-2 for more details. Data sources indicated with \*\* are described in A2 Supporting Information.

Category	Predictor	Code	Units	Rationale	Reference	Data source
<i>NATURAL</i>						
Geomorphic	Reach slope	<i>Slope</i>	%	Determines substrate size, water velocity; important predictor of cold water species in WEMAP sites	Kaufmann <i>et al.</i> , 1999; Pont <i>et al.</i> , 2009; Poff <i>et al.</i> , 2010a	NHDPlusv2
	Valley confinement (stream channel sinuosity)	<i>Confine</i>	-	Influences hyporheic flow; alternative measure of channel confinement	Poole & Berman, 2001	WEMAP, NRSA
	Baseflow index	<i>Baseflow</i>	fraction	Buffers against low flows; provides cold water from aquifers	Poff & Allan, 1995; Poff <i>et al.</i> , 2010a; Esselman <i>et al.</i> , 2013	Wolock, 2003
Local habitat	Sand and fine substrate	<i>Substrate</i>	%	Substrate influences hyporheic exchange	Webb <i>et al.</i> , 2008	WEMAP, NRSA
	Riparian cover	<i>Riparian</i>	Fraction (sum of ground, mid and canopy layers; areal proportion)	Insulates stream temperatures by blocking solar radiation, reducing atmospheric heat exchange; traps sediment	Gregory <i>et al.</i> , 1991; Naiman <i>et al.</i> , 1992; Poole & Berman, 2001	WEMAP, NRSA
	Mean August stream temperature	<i>RchStreamT</i>	°C	Physiological constraint for ectothermic species	Eaton & Scheller, 1996; Rieman <i>et al.</i> , 2007; Wenger <i>et al.</i> , 2011; Isaak <i>et al.</i> , 2015	NorWeST
	Mean annual runoff	<i>RCHSLOPE</i>	(m <sup>3</sup> /s/km <sup>2</sup> ): Mean Annual Flow (m <sup>3</sup> /s) / Upstream drainage area (km <sup>2</sup> )	Predictor of habitat size and species richness; influences stream temperature	Xenopolous & Lodge, 2006; Poole & Berman, 2001	NHDPlus

Category	Predictor	Code	Units	Rationale	Reference	Data source
<i>ANTHROPOGENIC</i>						
Sedimentation	Substrate embeddedness	<i>RchDSED_Embed</i>	%	Fine particulate deposition reduces levels of hyporheic dissolved oxygen	Packman & MacKay, 2003	WEMAP, NRSA
	Cumulative sediment	<i>DSED_Sed</i>	(tons/year/km <sup>2</sup> , HW)	Affects turbidity, availability of pool habitat and suitability of substrate for spawning.	Allan, 2004 (see other refs in Allan)	**
Nutrient enrichment	Cumulative nitrogen	<i>CatDNE_N</i>	(kg/year/km <sup>2</sup> , HW)	Key component of nutrient enrichment that may impair water quality and dissolved oxygen levels	Carpenter <i>et al.</i> , 1998; Allan, 2004	**
	Cumulative phosphorus	<i>CatDNE_P</i>	(kg/year/km <sup>2</sup> , HW)	Along with nitrogen, contributes to nutrient enrichment that may impair water quality and dissolved oxygen levels	Carpenter <i>et al.</i> , 1998; Allan, 2004	**
Hydrologic alteration	Flow modification	<i>CatDHA_FlowMod</i>	fraction	Changes to the natural flow regime including altered magnitude and frequency of high flows affect habitat through nutrient and sediment transport, floodplain interactions, thermal regimes, and connectivity	Poff <i>et al.</i> , 1997; Allan, 2004; Caissie, 2006; Poff & Zimmerman, 2010; Grill <i>et al.</i> , 2015; Fitzhugh & Vogel, 2010; Graf, 1999; Theobald <i>et al.</i> , 2010	**
	Canals	<i>CatDHA_Canals</i>	fraction	Measure of hydrologic alteration	Falcone <i>et al.</i> , 2010	**
Contaminant pollution	Mines	DCP_Mines	(%, HW)	Contributes to contaminant pollution, increases concentrations of heavy metals with implications for fish biology and survival	Allan, 2004; Clements <i>et al.</i> , 2000; Falcone <i>et al.</i> , 2010; Esselman <i>et al.</i> , 2011; Daniel <i>et al.</i> ,	**

Category	Predictor	Code	Units	Rationale	Reference	Data source
	NPDES	DCP_Discharge	(# sites/km2, HW)	Contributes to contaminant pollution involving heavy metals, synthetics and toxic organics	2014 Allan, 2004; Falcone <i>et al.</i> , 2010; Esselman <i>et al.</i> , 2011	**

Table A2 - 2. Summary of contributions of natural and anthropogenic predictors of cold- and cool-water fish occurrence. Predictor contributions indicate the relative influence of a predictor to the species distribution model and sum to 100%. Predictor ranks are indicated in parentheses. Blank entries indicate the predictor is not included in the species model. Predictors are sorted by mean overall importance for all species. Rch = reach; Cat = catchment. Anthropogenic predictors are associated with disturbance mechanisms as follows: DSED = sedimentation, DNE = nutrient enrichment, DCP = contaminant pollution, DHA = hydrologic alteration. See Table 3-2 for predictor explanations.

<b>Predictor</b>	<b>Mountain Sucker</b>	<b>Mottled Sculpin</b>	<b>Longnose Dace</b>	<b>Speckled Dace</b>	<b>Cutthroat Trout</b>	<b>Rainbow Trout</b>
<i>CatDNE_N</i>	18.29 (2)	10.63 (3)	22.35 (1)	19.95 (2)	12.10 (3)	17.68 (2)
<i>RchSlope</i>	28.44 (1)	18.72 (1)	21.05 (3)	15.15 (3)	4.89 (9)	13.09 (3)
<i>RchStreamT</i>	4.45 (6)	8.43 (5)	12.19 (4)	34.81 (1)	10.36 (5)	21.58 (1)
<i>RchDSED_Embed</i>	1.91 (12)	8.74 (4)	0.75 (12)	4.88 (5)	10.54 (4)	8.72 (5)
<i>CatMAR</i>	7.50 (4)	10.90 (2)	1.67 (7)	3.76 (8)	17.97 (1)	4.94 (7)
<i>CatBaseflow</i>	14.69 (3)	5.75 (9)	1.00 (10)	4.51 (6)	12.25 (2)	4.67 (9)
<i>RchRiparian</i>	2.64 (10)	5.18 (10)	0.72 (13)	4.13 (7)	7.99 (6)	7.27 (6)
<i>RchConfine</i>	5.57 (5)	7.61 (7)	0.87 (11)	1.09 (11)	7.36 (7)	3.10 (10)
<i>RchSubstrate</i>	1.72 (13)	7.85 (6)	1.15 (8)	0.93 (13)	6.57 (8)	12.09 (4)
<i>CatDNE_P</i>	1.64 (14)	3.98 (11)	4.89 (6)	1.58 (9)	3.43 (11)	4.93 (8)
<i>CatDHA_FlowMod</i>	3.74 (8)	1.39 (13)	9.92 (5)	6.09 (4)	1.99 (12)	0.04 (14)
<i>CatDSED_Sediment</i>	2.29 (11)	6.94 (8)	0.06 (14)	1.48 (10)	4.15 (10)	1.39 (11)
<i>CatDHA_Canals</i>	3.90 (7)	0.79 (14)	22.27 (2)	1.08 (12)		0.28 (12)
<i>CatDCP_Mines</i>	3.22 (9)	3.07 (12)	1.09 (9)	0.56 (14)	0.40 (13)	0.21 (13)
<i>CatDCP_Discharge</i>						

# Mountain Sucker

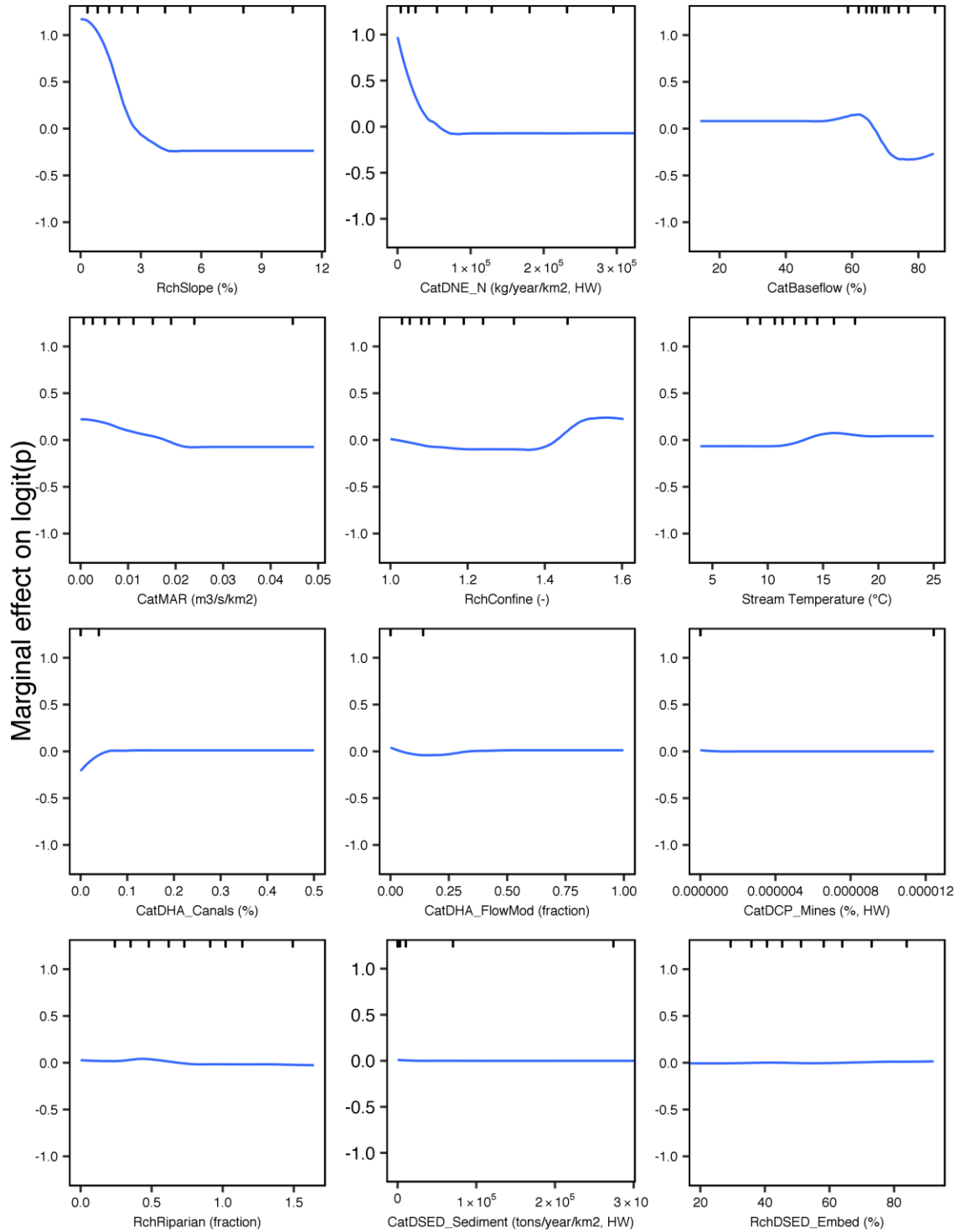


Figure A2 - 1. Partial dependence plots for mountain sucker.

# Mottled Sculpin

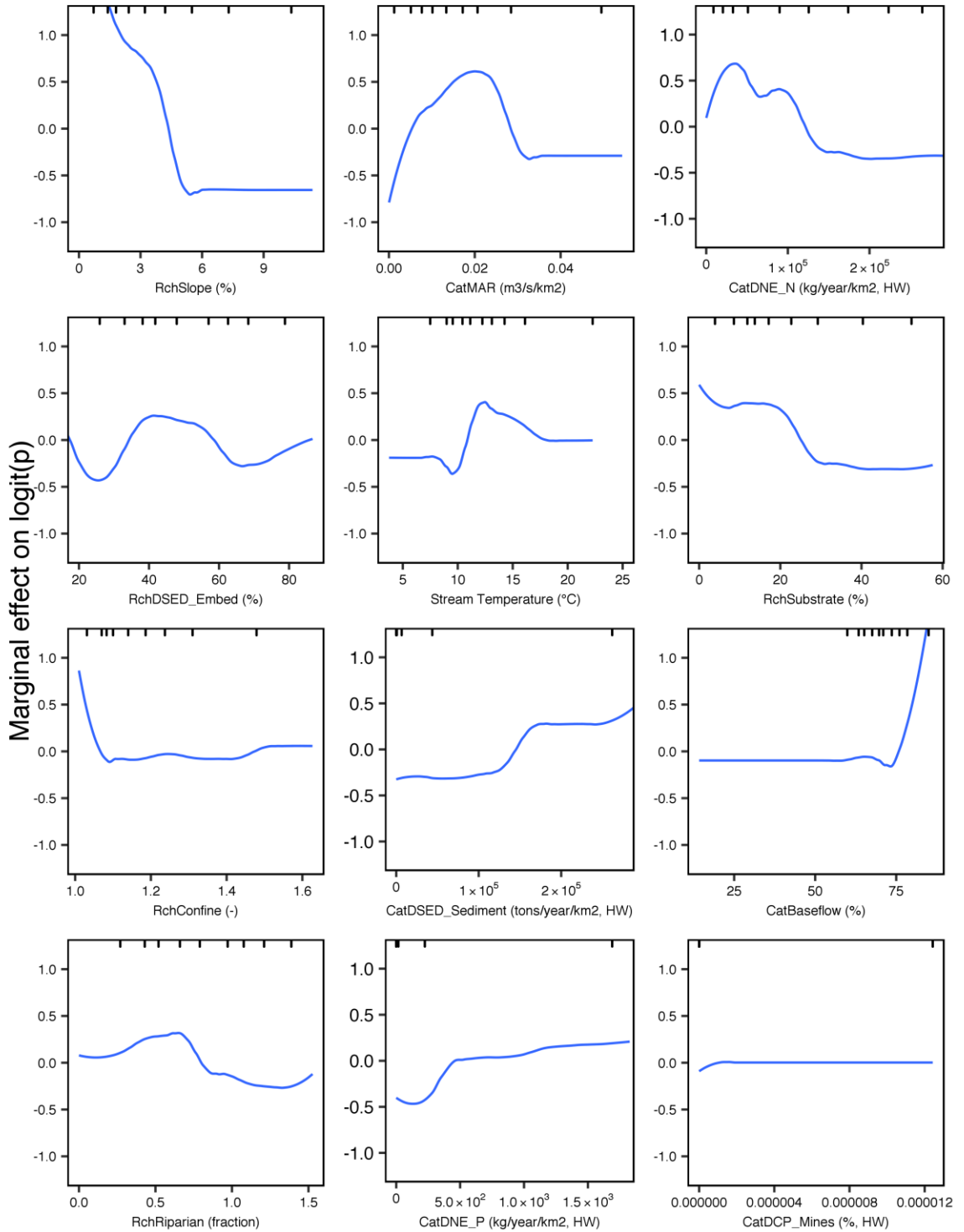


Figure A2 - 2. Partial dependence plots for mottled sculpin.

# Longnose Dace

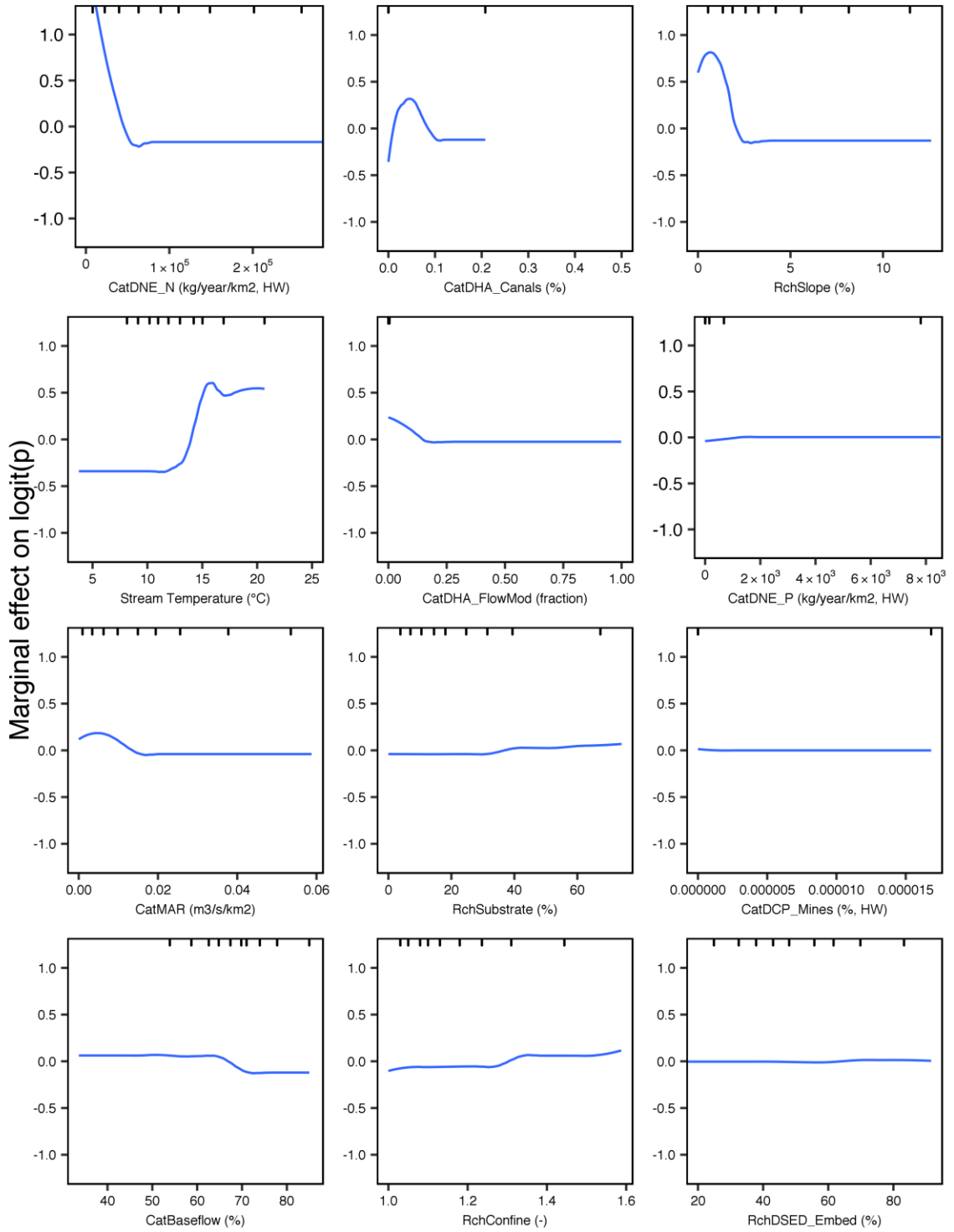


Figure A2 - 3. Partial dependence plots for longnose dace.



## Speckled Dace

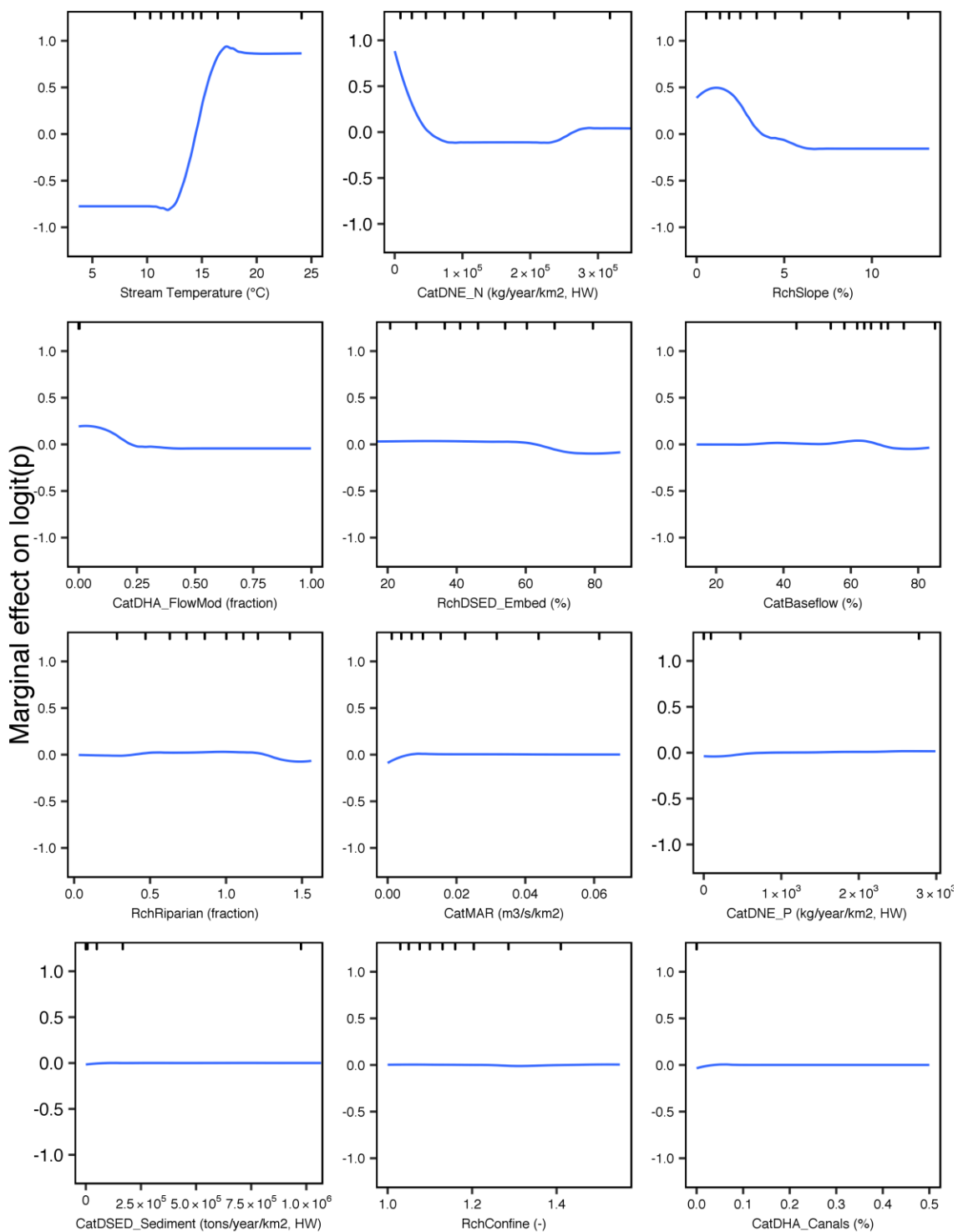


Figure A2 - 4. Partial dependence plots for speckled dace.

## Cutthroat Trout

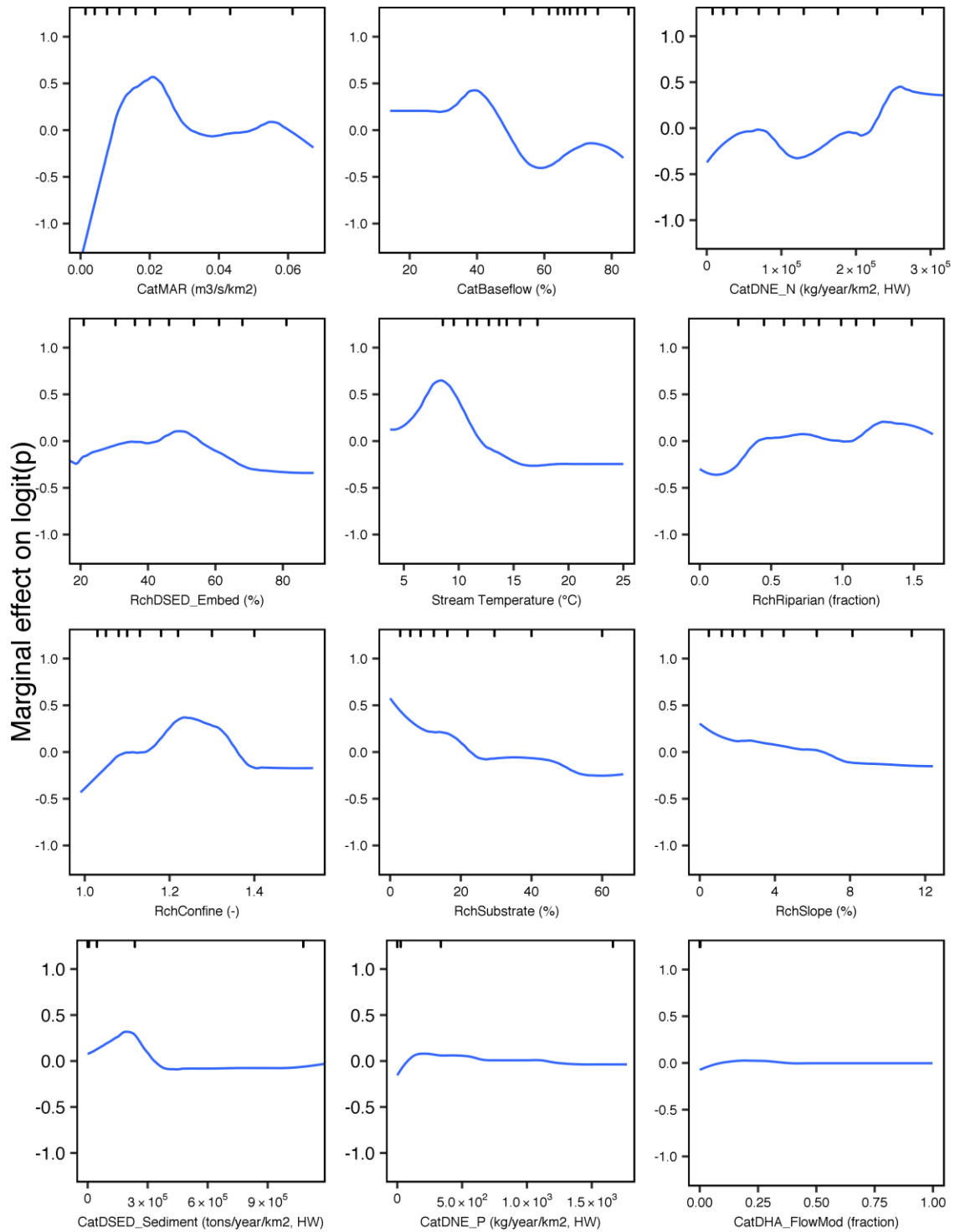


Figure A2 - 5. Partial dependence plots for cutthroat trout.

# Rainbow Trout

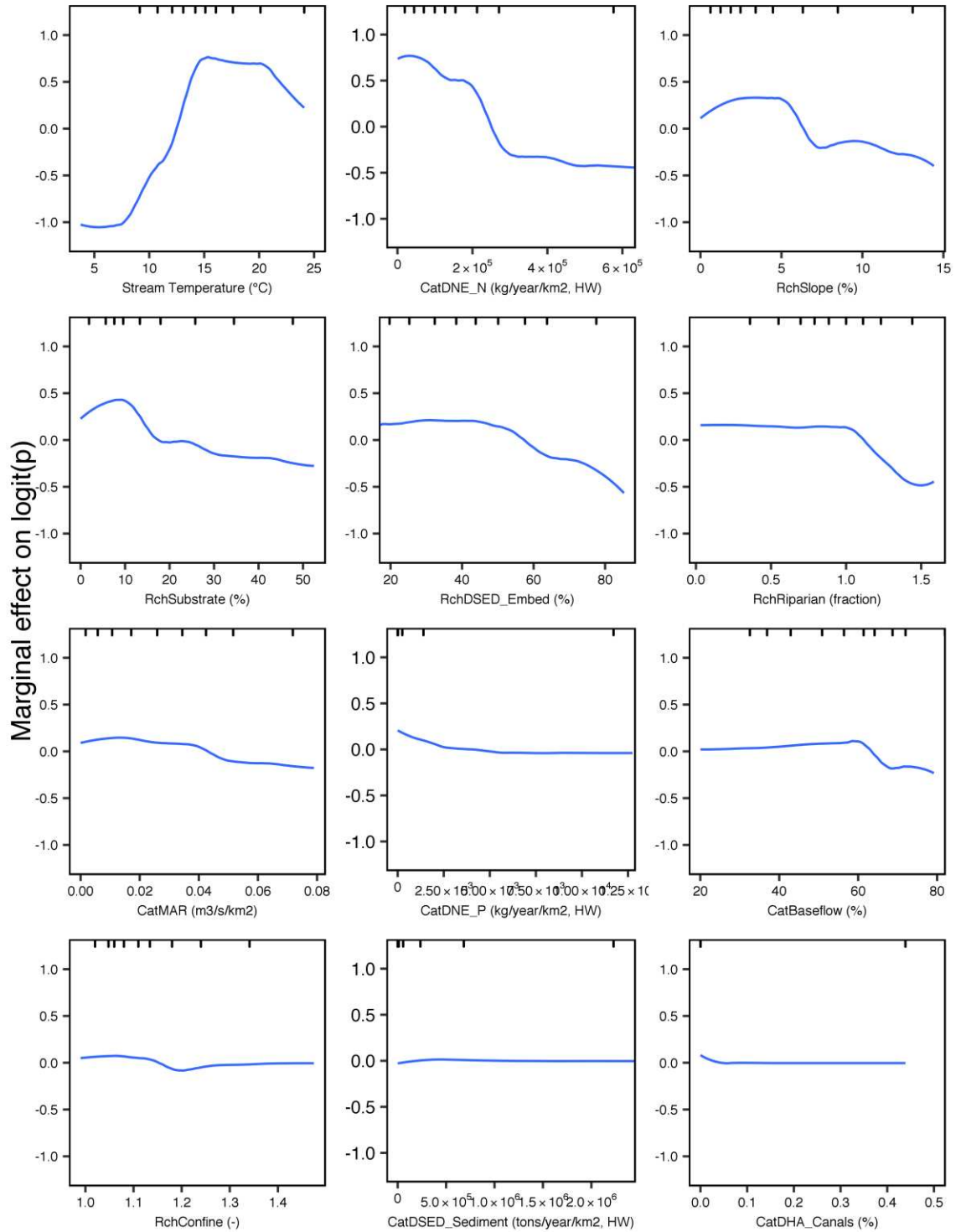


Figure A2 - 6. Partial dependence plots for rainbow trout.

### **A.3. Supporting information for vulnerability analysis**

#### *Stream temperature data*

This research was supported by high quality, publically available data. We acquired modeled stream temperature data from <http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST>. Stream temperature models produced by NorWeST utilize an extensive suite of landscape and hydrological predictor variables to estimate stream temperature at high resolution (see [http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST/downloads/NorWeST\\_StreamTemperatureModelDescription.pdf](http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST/downloads/NorWeST_StreamTemperatureModelDescription.pdf) for metadata). Percent canopy cover from the 2001 National Land Cover Database (NLCD) is an input to the stream temperature model. Visual inspection of canopy cover estimates that were attributed to stream reaches indicated that the NCLD-based estimate was a relatively crude surrogate for riparian cover. We therefore elected to use the riparian cover data obtained from the EPA field surveys as our descriptor of riparian vegetation at the reach scale because it was thought to better reflect on-the-ground vegetation conditions that are relevant to stream shading and temperature regulation.

#### *Species distribution models*

Thermal niches for rainbow trout and cutthroat trout revealed differences in thermal optima and also differences in the relationship between species occurrence and stream temperature, particularly at warmer temperatures. Numerous studies have reported that rainbow trout, in relation to cutthroat trout in particular, are more tolerant of warm temperatures (Eaton & Scheller, 1996; Roberts *et al.*, 2013), can outperform and outcompete cutthroat trout at warm temperatures (Bear, McMahon & Zale, 2007), and occur at warmer locations (Wenger *et al.*, 2011). Non-lethal responses of rainbow trout at temperatures that are high but below thermal limits are reflected in the model via decreased probabilities of occurrence. We further imposed a

lethal temperature limit to ensure that predictions for stream temperatures exceeding 24 °C (Eaton & Scheller, 1996) would be classified as absences in the rainbow trout SDMs. Similar adjustments were not needed for cutthroat trout because occurrence probabilities at warm temperatures were consistently below our classification threshold (i.e. absences).

#### *Sensitivity analysis*

We performed a sensitivity analysis to disentangle the role of temperature versus streamflow in driving species' range-wide vulnerabilities. Holding MAF at baseline levels while using projected ST for 2080 we found that our range-wide vulnerability estimates for cutthroat trout were 1.8% less for cutthroat trout and 0.7% greater for rainbow trout compared to estimates obtained using both projected MAF and ST.

#### *Stream survey data*

Both of the fish species included in this analysis exist in anadromous forms. We excluded from our records of occurrence data those entries flagged as anadromous because the life histories of these individuals may include habitat associations that differ from those of resident individuals (Behnke, 2002). To address potential spatial autocorrelation from repeat site visits, we excluded multiple observations that were attributed to the same reach. Only the most recent observations were used in cases where multiple visits occurred.

#### *Precision of substrate metrics*

Stream substrate conditions were sampled as part of EPA surveys. Embeddedness was estimated using repeated visual assessment of substrate conditions at 11 equally-spaced transects along a stream reach. Results taken from an analysis by Kaufmann *et al.* (1999) of sampling precision of EPA field habitat survey methods are provided here to enable comparisons between substrate metrics. The analysis was based on data collected as part of a U.S. EPA EMAP survey

of several hundred streams in Oregon (Herlihy *et al.*, 1997). The information is relevant for assessing the reliability and precision of embeddedness in comparison to other substrate metrics. Two metrics of precision are provided below. The first,  $\sigma_{rep}$ , or root mean square error (RMSE) is analogous to pooled standard deviation of repeated measurements, with lower values indicating greater precision of measurement. The second, signal to noise ratio (S/N), compares variance in the substrate metric due to regional sampling of streams with variance attributable to within-season field measurement. Higher values of S/N reflect greater metric precision relative to regional variation (Kaufmann *et al.*, 1999). The results suggest that embeddedness is a suitable substrate metric for the purposes of this analysis given that measurements have sufficient precision (RMSE). The S/N ratio for embeddedness was the second largest of the four metrics considered. Percent fines had the lowest RMSE and S/N of all substrate metrics.

Table A3 - 1. Precision of selected stream reach substrate metrics. Results are for stream surveys (n=44 with 22 replicates) conducted in Oregon using the same field habitat survey methods employed in WEMAP and NRSA surveys that were utilized in the fish vulnerability analysis.  $S/N = \sigma_{st}(yr)/\sigma_{2rep}$ . Data are from Table 10 in (Kaufmann *et al.*, 1999).

<b>Substrate metric</b>	<b>RMSE = <math>\sigma_{rep}</math> (in units of metric)</b>	<b>S/N</b>
% substrate Embedded – mid-channel + margin (used in this analysis)	9.5	7.7
% substrate - Sand	7.9	0.1
% substrate – Fines (Silt, Clay, and Muck)	7.4	15
% substrate – Sand + Fines	11	7.1

Table A3 - 2. Overview of regional studies in the western United States that assessed range-wide impacts of climate change on rainbow trout and cutthroat trout.

Region	Species	Findings	Variables <sup>1</sup>	Key differences	Reference
Northern Rocky Mountains	Cutthroat trout	-58% number of refugia by 2080 assuming no brook trout, - 78% number of refugia by 2080 with 50% brook trout invasion. By 2080, median refugia size decreases by 23% and 10%, respectively, under brook trout scenarios.	ST, slope, habitat size, B	Investigated climate refugia by modeling contiguous sections of coldwater habitat. Hydrologic variables not explicitly considered in distribution model.	Isaak <i>et al.</i> (2015)
Upper Colorado River Basin	Cutthroat trout	No high elevation populations found to be at risk from acute mortality due to warming; however, only 37% of populations projected to persist to 2080, largely due to stochastic disturbances.	ST, Ha, Population, network fragmentation, disturbances	Focused explicitly on conservation populations that have been restricted to fragmented, high elevation streams. High temperatures play a relatively minor threat to these populations in comparison to catastrophic events like wildfire, debris flows, and hydrologic extremes (e.g. stream drying/freezing).	Roberts <i>et al.</i> (2013)
Interior western US (historic cutthroat range)	Cutthroat trout	Substantial variability due to choice of GCM: -28% suitable stream miles by 2040, -58% by 2080 under composite model projections; compared to -33% by 2080 under PCM1 model projections versus -70% for MIROC3.2 model projections	AT, Hy, B, Ha	Biotic interactions accounted for upwards of 33% of predicted decline in cutthroat distribution	Wenger <i>et al.</i> (2011)
	Rainbow trout	-13% suitable stream miles by 2040, -35% by 2080			

<sup>1</sup> ST = stream temperature; AT = air temperature; Hy = hydrology; B = biotic interactions; Ha = habitat; A = anthropogenic

Historic native ranges of cutthroat trout subspecies	Colorado River cutthroat, Bonneville cutthroat, Westslope cutthroat	Large portion (65-73%) of currently occupied habitat considered to be high risk for Bonneville and Westslope cutthroat compared to 29% for Colorado River cutthroat.	AT, Hy, Disturbance (wildfire), population persistence	Derived composite index for estimating population risk based on existing population densities, habitat fragmentation, and projected changes in air temperature, winter flooding and wildfire. Greatest climate change threats posed by risk of floods and fires as opposed to increases in temperature.	Williams <i>et al.</i> (2009)
Continental United States	Rainbow trout	36.8% reduction in number of suitable sites	ST	Estimated maximum stream temperature at 764 sites using a nonlinear model and projected changes in thermally-suitable sites using methods similar to Eaton & Scheller (1996). Projected losses under a 2 x CO2 warming scenario are less severe compared to those obtained by Eaton & Scheller (1996) using air temperature.	Mohseni, Stefan and Eaton (2003)
Continental United States	Cutthroat trout	36.9% reduction in number of suitable sites			
Continental United States	Rainbow Trout	49.1% sites projected to become unsuitable for rainbow trout; large percentage of those losses occur in the Eastern US.	AT	Coarse resolution grid (3.75 x 3.75 degree) of future air temperature increases applied to baseline temperatures at USGS stations to project future temperatures. Fish distributions considered to be a function solely of thermal conditions. If occurrence records indicated that species was found within a GCM grid cell, that species was then assumed to occur at all USGS stations within that grid cell.	Eaton and Scheller (1996)



Rocky Mountain region	Cutthroat trout	40.2% reduction in number of suitable sites	AT	Using 22 °C as thermal limit, projected loss in suitable habitat from universally-applied temperature increases within air temperature isotherms.	Keleher and Rahel (1996)
		Reductions in area containing suitable thermal habitat of 16.8%, 35.6%, 49.8%, 62.0%, and 71.8% associated with 1, 2, 3, 4, 5 °C increases in air temperature			

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Table A3 - 3. Summary statistics for predictor variables used to develop species distribution models. ST and MAF data were acquired from publically available sources. Riparian cover and embeddedness metrics were collected through field sampling as part of stream surveys conducted by the US Environmental Protection Agency. Hydrologic Weighting scheme (HW) is described in A2.

<b>Species</b>	<b>Variable</b>	<b>Units</b>	<b>Minimum</b>	<b>Median</b>	<b>Mean</b>	<b>Maximum</b>
Cutthroat trout	Stream temperature (ST)	°C	3.8	12.7	12.7	26.1
	Mean annual flow (MAF)	cfs	0.07	11.2	45.9	728.8
	Riparian cover (RC)	fractional cover, summed for ground, mid-, and canopy layers	0	0.8	0.9	2.8
	Embeddedness (Embed)	%	2.0	46.3	49.2	100
	Nitrogen (N)	kg/year/km <sup>2</sup> , HW	206	96536	155787	4311484
	Baseflow (BFI)	%	14.2	65.9	63.7	85
Rainbow trout	Stream temperature (ST)	°C	3.8	14.2	14.2	24.1
	Mean annual flow (MAF)	cfs	0.0	11.5	39.7	672.0
	Riparian cover (RC)	fractional cover, summed for ground, mid-, and canopy layers	0	0.89	0.91	2.1
	Embeddedness (Embed)	%	2	43.8	46.0	100
	Nitrogen (N)	kg/year/km <sup>2</sup> , HW	605	127598	256039	4923671
	Baseflow (BFI)	%	20	56.2	53.5	82.0

Table A3 - 4. Supplemental performance measures and parameterizations of species distribution models for assessing regional climate-induced vulnerability and local vulnerability to climate and land use scenarios. Cross-validated performance measures were obtained using withheld subsets of occurrence data. AUC = area under the receiver operating characteristic curve; CCR = correct classification rate. CCR is useful for examining overall accuracy (Olden, Jackson & Peres-Neto, 2002). The significance of boosted regression tree model parameters is described in (Elith, Leathwick & Hastie, 2008).

<b>Species</b>	<b>Model</b>	<b>Cross-validated performance</b>	<b>Model parameters</b>
Cutthroat trout	Range-wide	AUC: 0.67 CCR: 60%	n.trees = 1000 interaction depth = 2 shrinkage = 0.0005
	Local	AUC: 0.71 CCR: 65%	n.trees = 9600 interaction depth = 3 shrinkage = 0.0005
Rainbow trout	Range-wide	AUC: 0.76 CCR: 66%	n.trees = 8600 interaction depth = 2 shrinkage = 0.0001
	Local	AUC: 0.81 CCR: 73%	n.trees = 5650 interaction depth = 3 shrinkage = 0.001

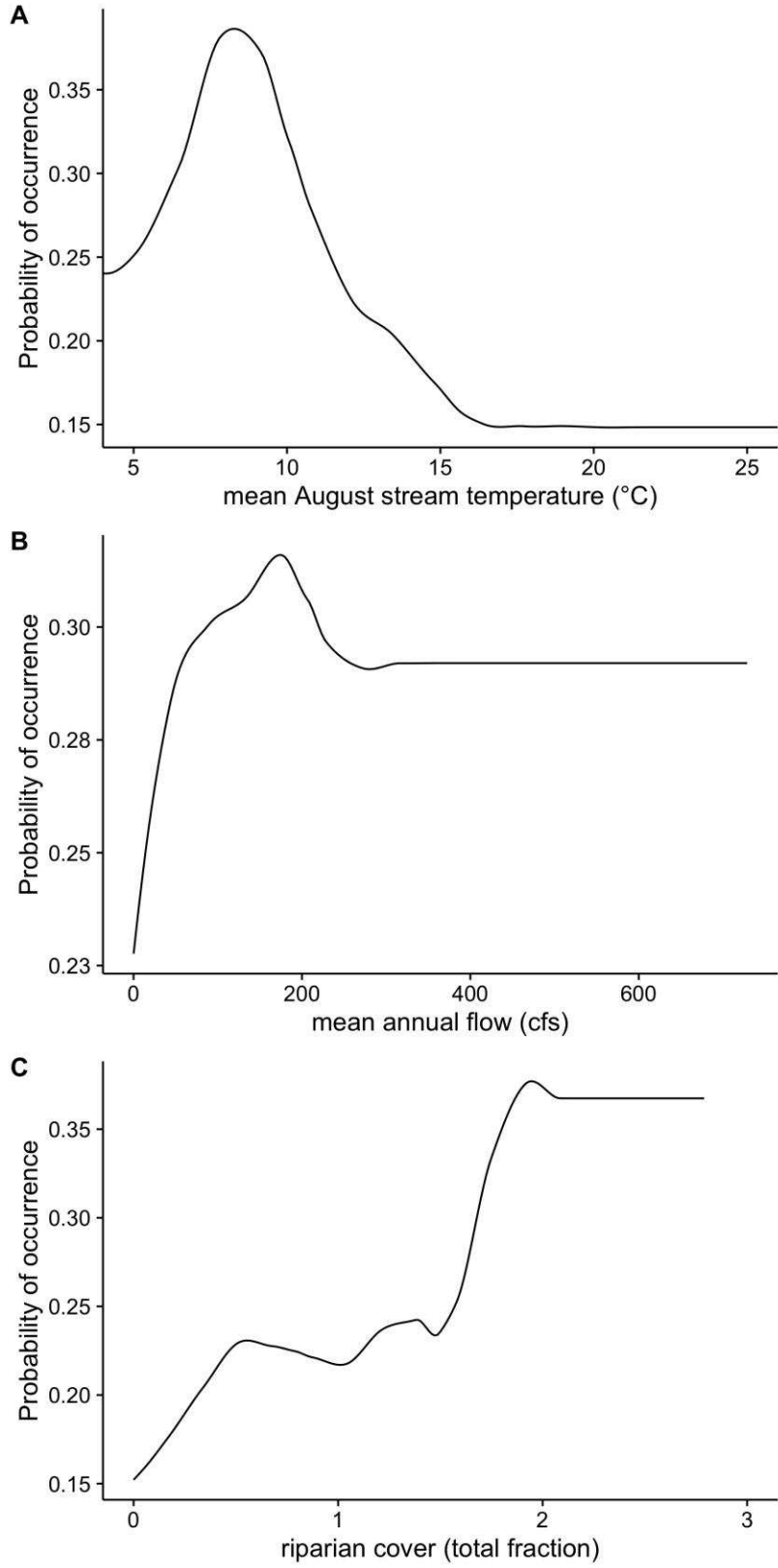


Figure A3 - 1. Partial dependence plots for the cutthroat trout species distribution model (SDM).

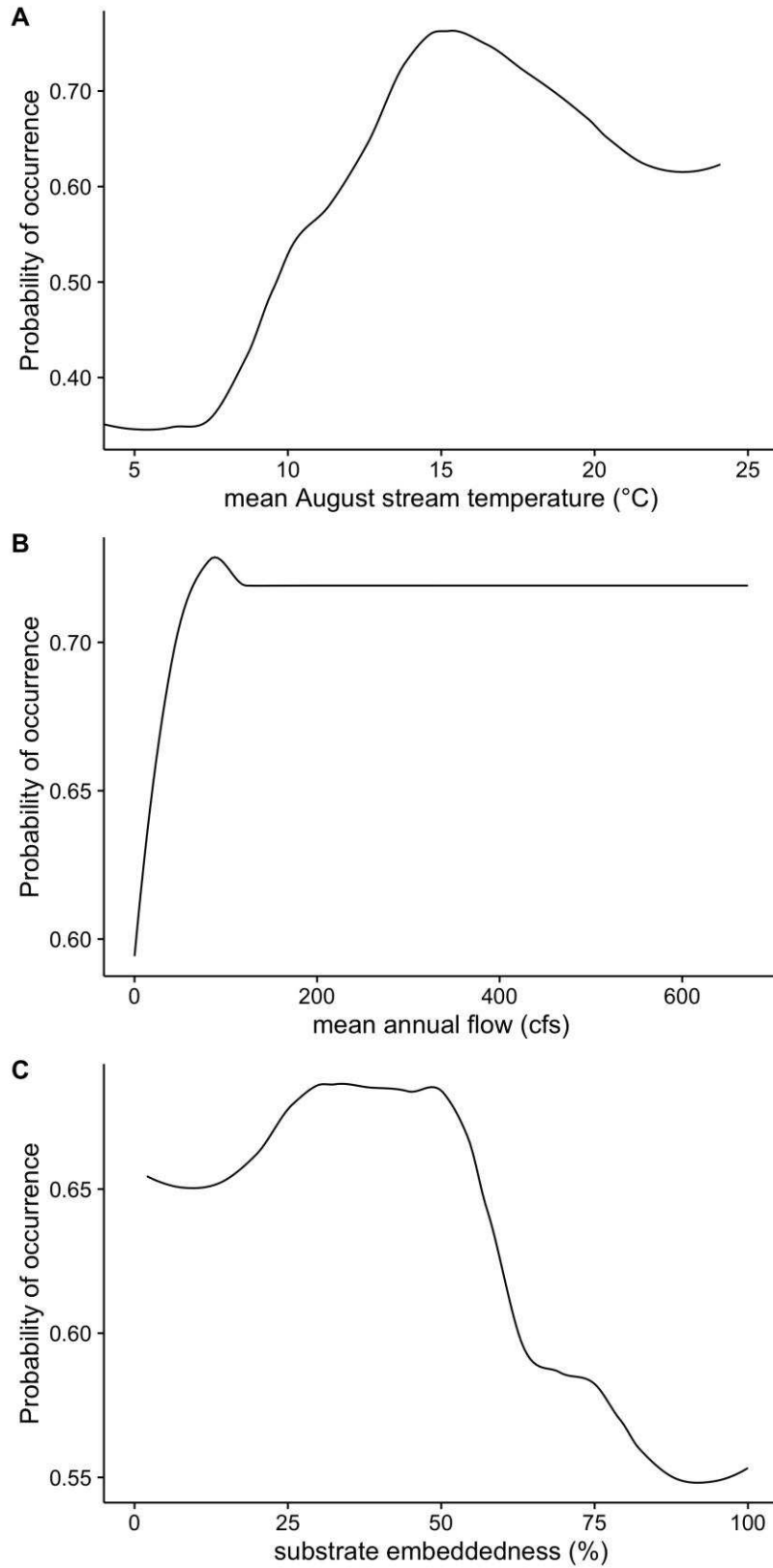


Figure A3 - 2. Partial dependence plots for the rainbow trout species distribution model (SDM).

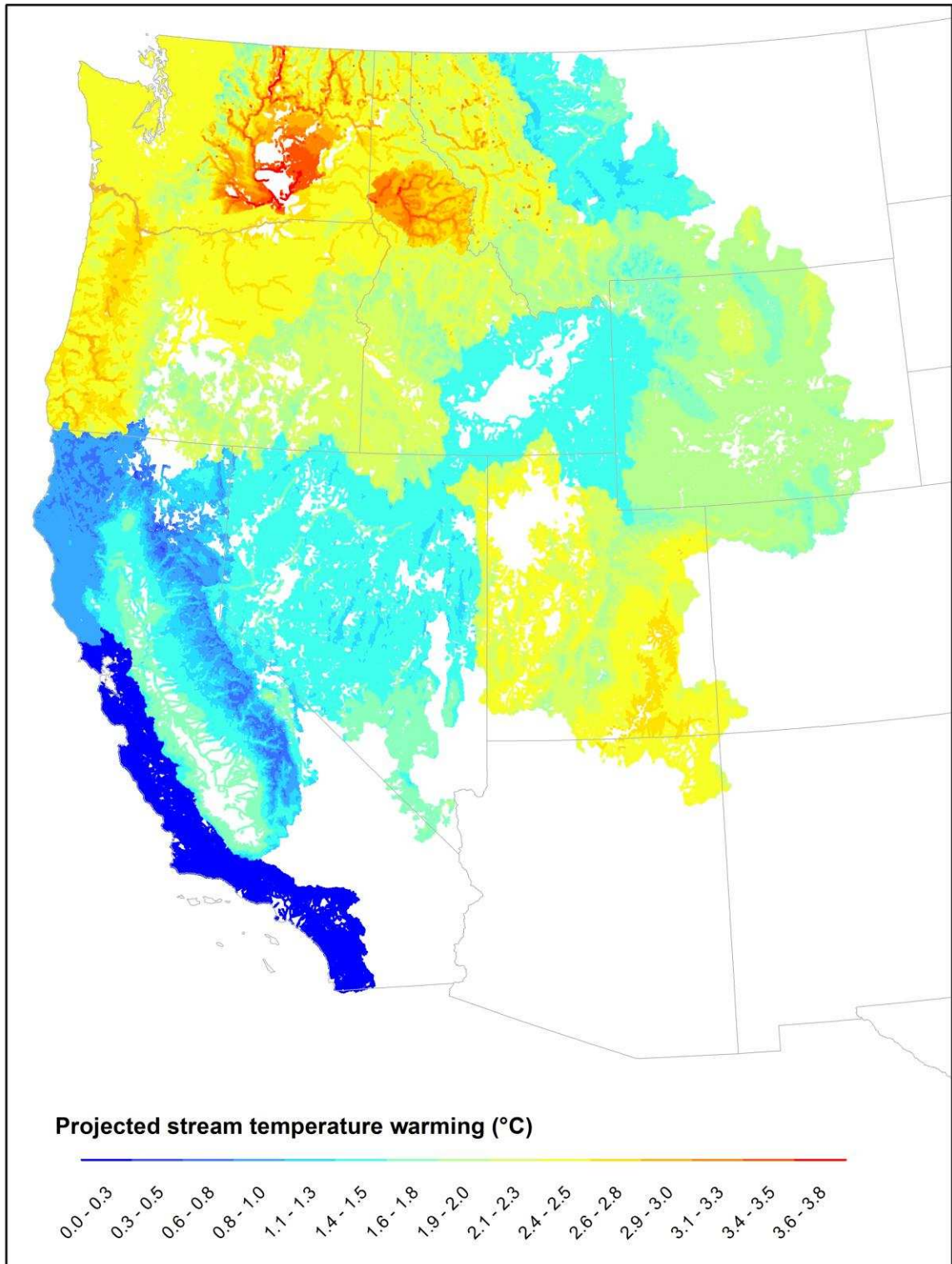


Figure A3 - 3. Projected stream temperature warming for 2080. Magnitudes of warming are greatest in the Colorado River basin and Columbia River basin. Unlike many inland streams, coastal streams in California are relatively buffered from climate-warming. Individual streams are not visible at this extent but exhibit spatial variability in the magnitude of projected warming.

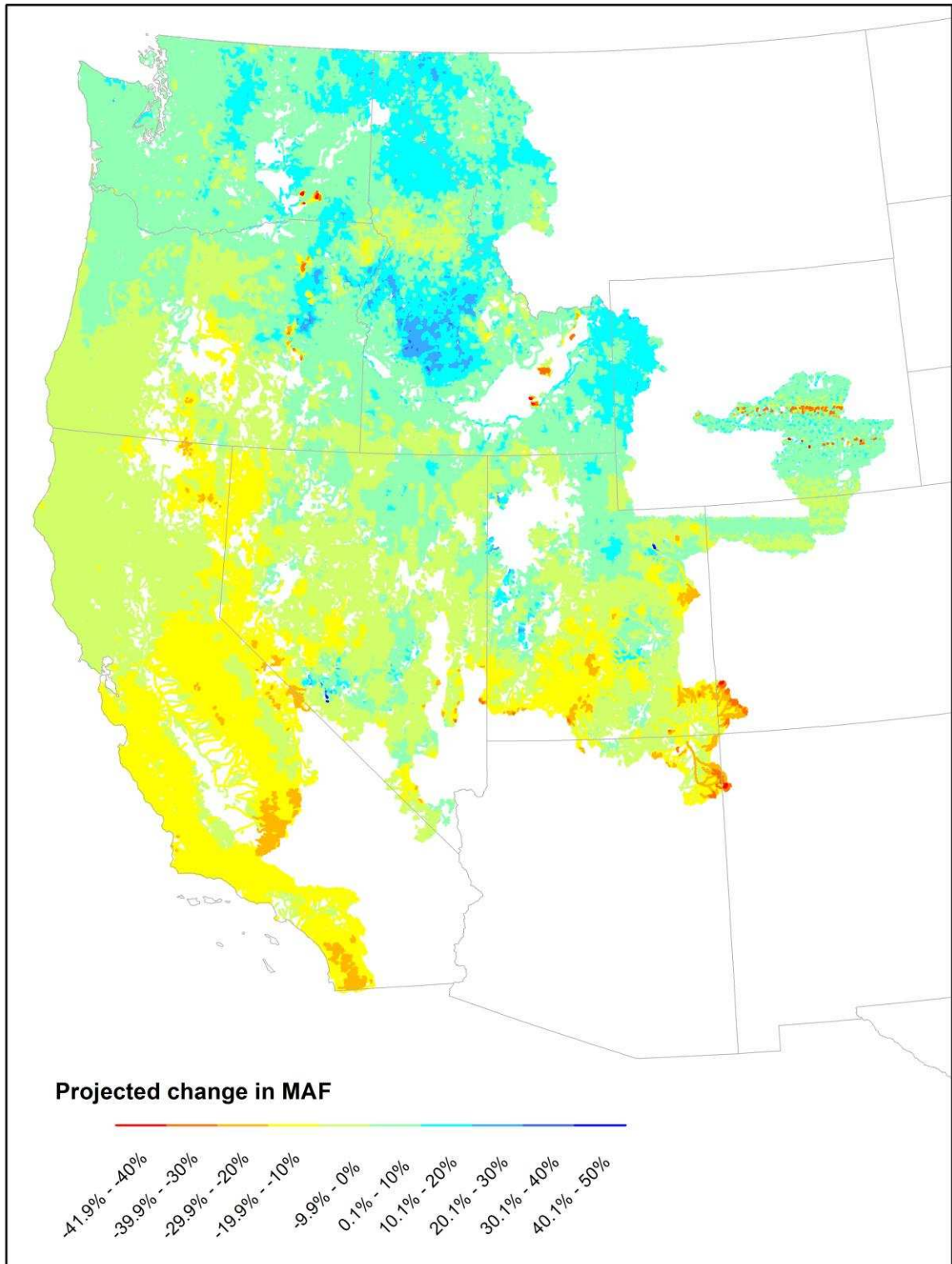


Figure A3 - 4. Projected change in mean annual flow (MAF) for 2080. Historic and future streamflow was simulated using the Variable Infiltration Capacity (VIC) model (Wenger *et al.*, 2010). These streamflow metrics were acquired from [http://www.fs.fed.us/rm/boise/AWAE/projects/modeled\\_stream\\_flow\\_metrics.shtml#data](http://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml#data)

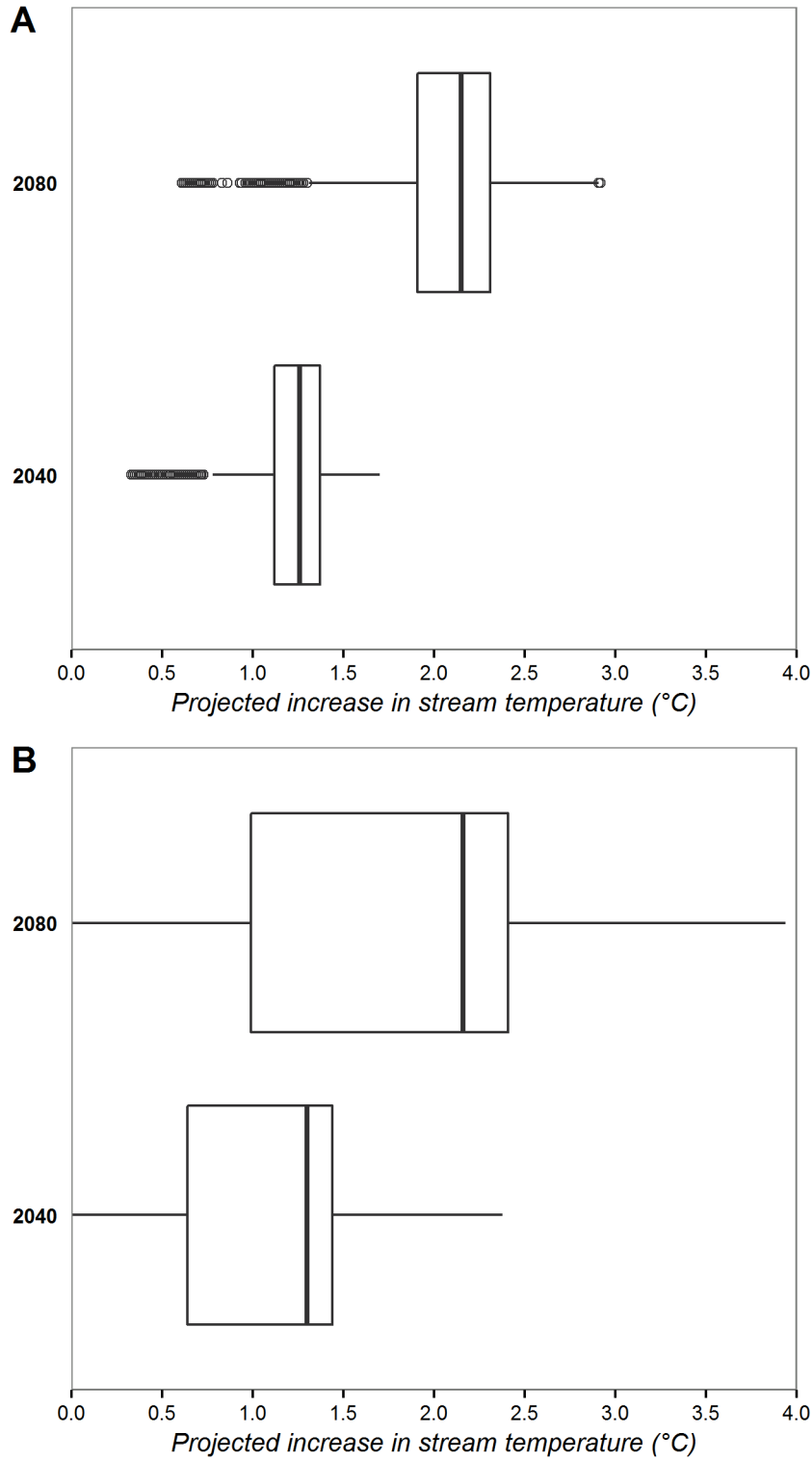


Figure A3 - 5. Projected increases in mean August stream temperature among currently suitable reaches for cutthroat trout (A) and rainbow trout (B) for 2040 and 2080. Projections are for the A1B scenario and were produced using a 10 model ensemble described in Isaak *et al.* (2015). Increases are relative to the baseline period (1993-2011).



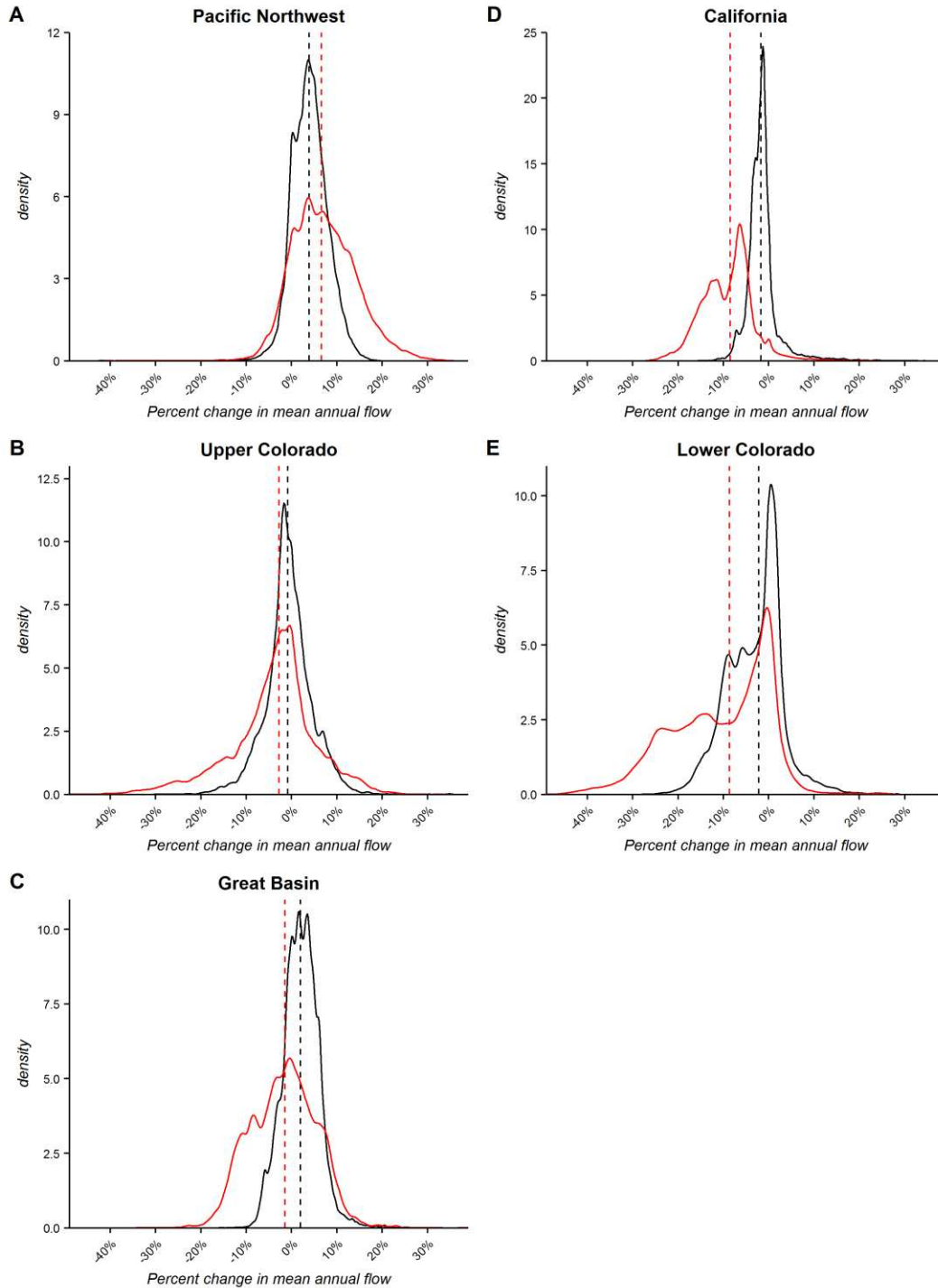


Figure A3 - 6. Distribution of projected changes in mean annual flow among stream reaches by major river basin. Density plots illustrate changes in mean annual flow by 2040 (black) and 2080 (red) with median values indicated with dashed lines. Considerable variability in projected changes is evident among reaches within river basins. Mean projections from a ten model ensemble were used to project climate scenarios under the A1B scenario. Stream flow metrics were derived from VIC model simulations that were routed within the NHDPlusV2 stream network (Wenger *et al.*, 2010). Data were acquired as part of the Western US Stream Flow Metric Dataset ([http://www.fs.fed.us/rm/boise/AWAE/projects/modeled\\_stream\\_flow\\_metrics.shtml](http://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml))

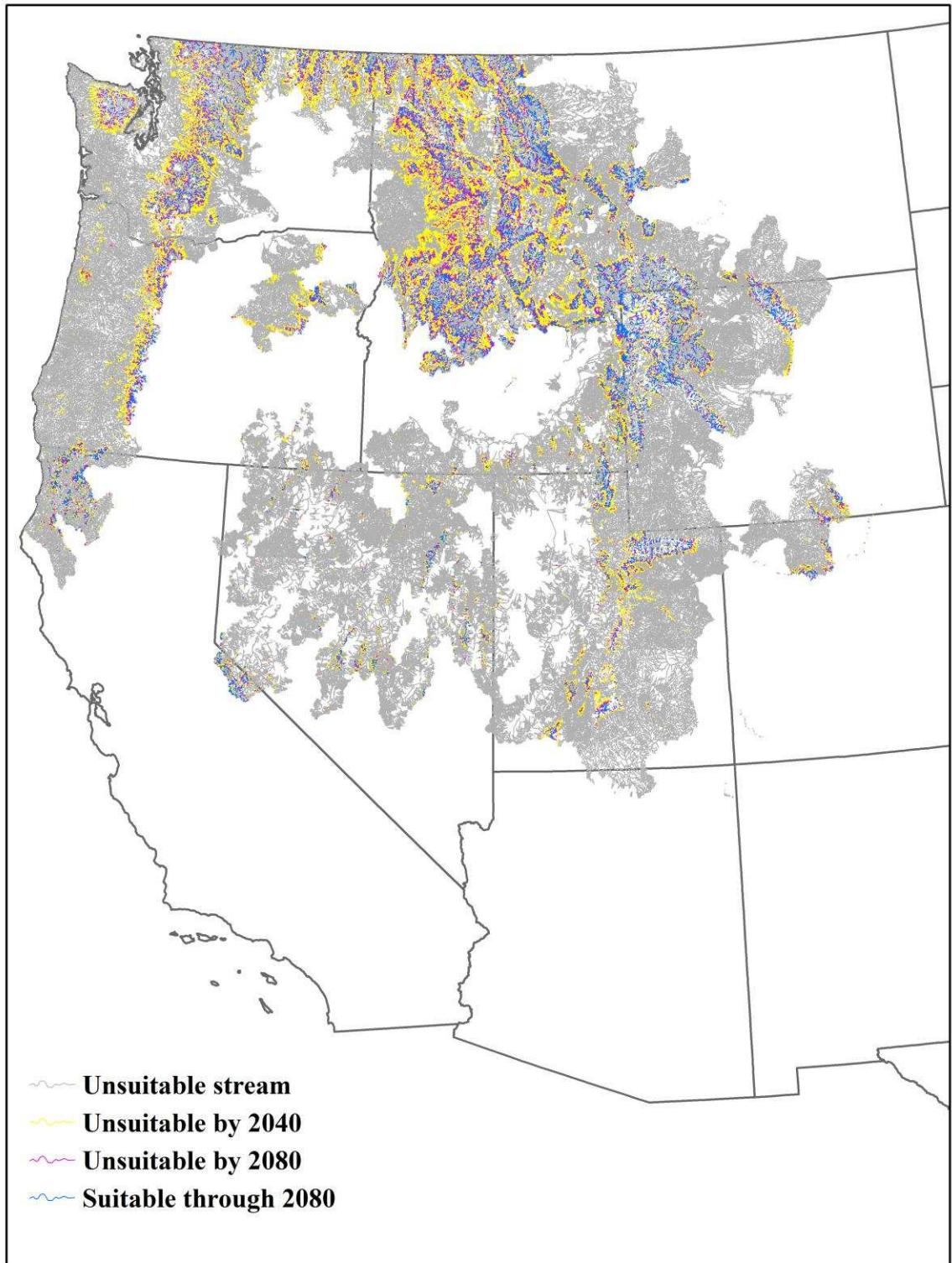


Figure A3 - 7. Projected losses of suitable habitat for cutthroat trout for 2040 and 2080 due to changes in summer stream temperature and mean annual flow. Habitat loss progresses upstream, producing a distinct elevational pattern.

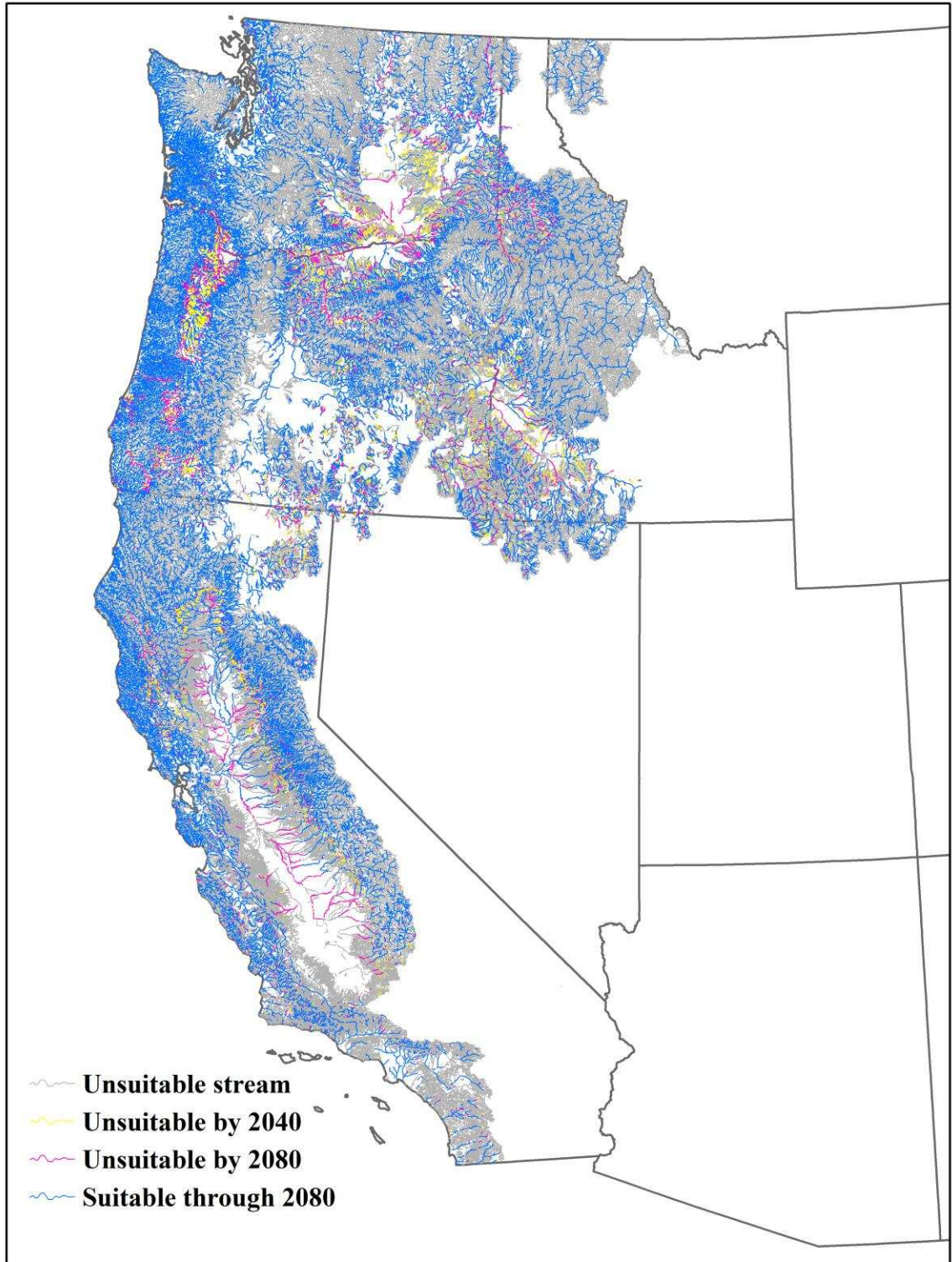


Figure A3 - 8. Projected losses of suitable habitat for rainbow trout for 2040 and 2080. Range-wide declines for rainbow trout appear modest (14%) but are high in central California, the Cascade Range and portions of the Pacific Northwest within the Columbia River basin.

Table A3 - 5. Results of habitat fragmentation analysis for cutthroat trout. Contiguous sections of suitable habitat (i.e. clusters) refer to lengths of adjacent thermally suitable habitat. Projected decreases in cluster length indicate that cutthroat trout will be confined to smaller, more isolated environments where they are likely to be exposed to a variety of additional stressors.

<b>Period</b>	<b>Number of clusters</b>	<b>Mean length (km)</b>	<b>Percent change</b>
<b>Present</b>	9928	14.01	
<b>2040</b>	9763	11.28	-19.5%
<b>2080</b>	9292	9.9	-29.3%

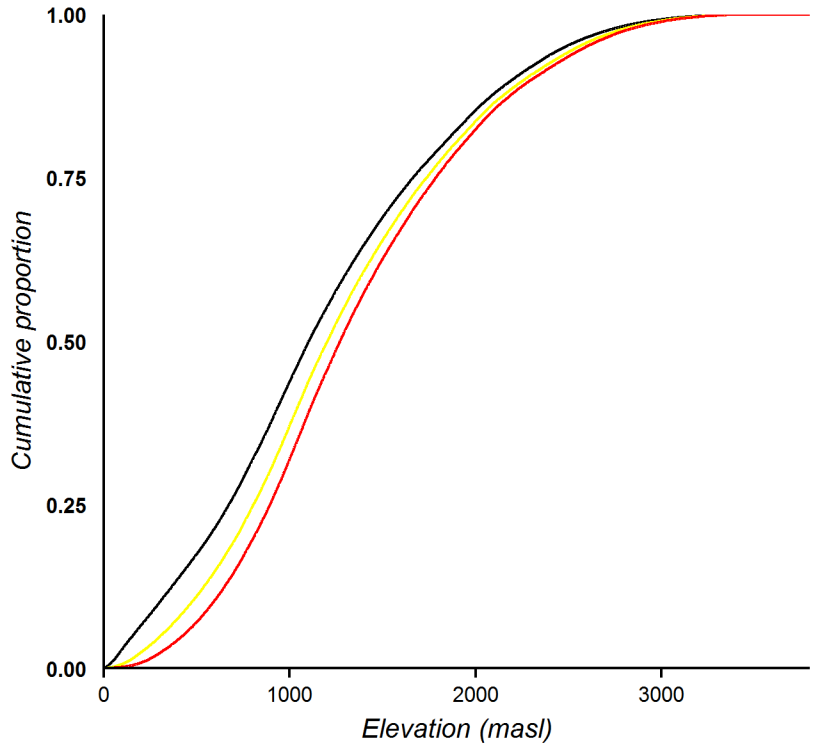


Figure A3 - 9. Changes in cutthroat trout distribution by elevation. Warming stream temperatures drive losses of formerly suitable habitat (black) at low elevations by 2040 (yellow) with more substantial elevational shifts in cutthroat trout distribution projected by 2080 (red).

Table A3 - 6. Results of decision-scaling vulnerability of cutthroat trout for climate adaptation scenarios involving riparian vegetation cover. Percentages reflect differences in estimated vulnerability for each riparian vegetation scenario relative to the baseline scenario.

<b>Vulnerability measure</b>	<b>Riparian vegetation scenario</b>	
	<b>-25% riparian cover</b>	<b>+25% riparian cover</b>
Minimum vulnerability	-	-
25th percentile	+6.7%	-29.2%
50th percentile	+17.8%	-21.5%
Mean	+17.3%	-24.1%
75th percentile	+17.7%	-23.8%
Maximum vulnerability	+19.2%	-22.1%

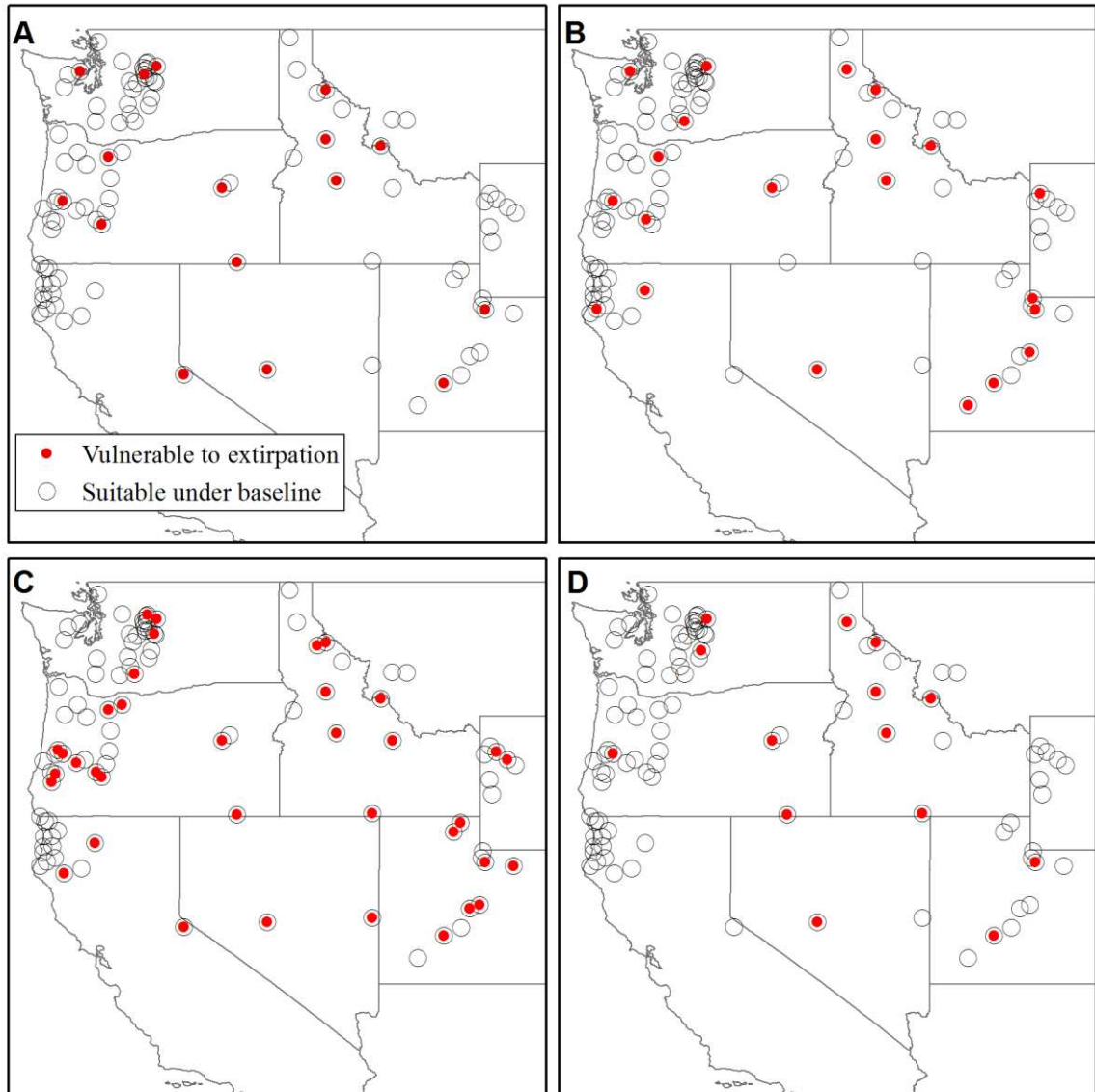


Figure A3 - 10. Vulnerability of cutthroat trout to local extirpation under global change scenarios. In addition to projected changes in August stream temperature and mean annual flow (A), vulnerability is modeled as a function of decreased riparian cover (-50%; B), increased sedimentation (+50%; C), and increased nitrogen (+50%, D) relative to baseline levels. Sites modeled as suitable (i.e. where species presence is predicted) under baseline conditions are shown in all panels.

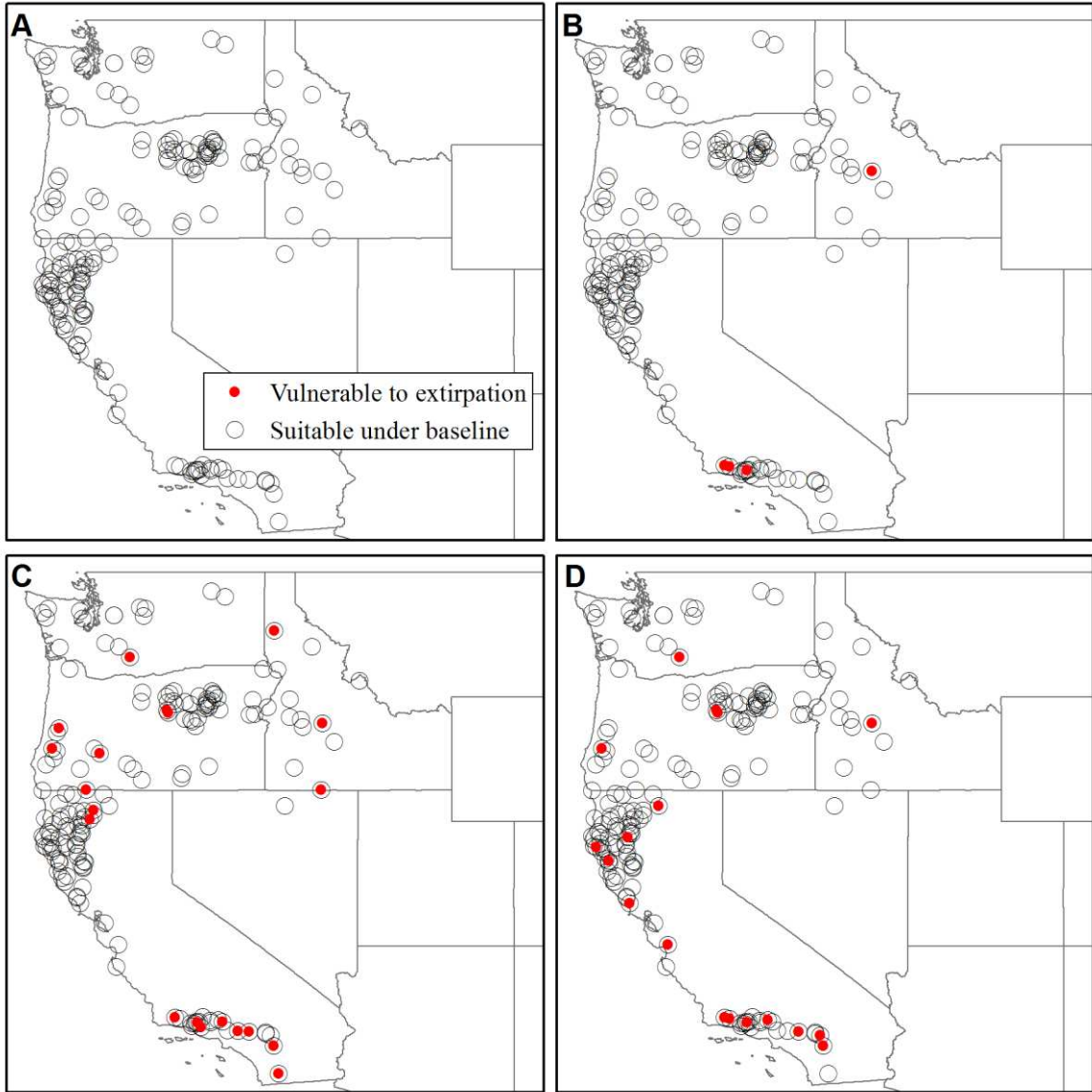


Figure A3 - 11. Vulnerability of rainbow trout to local extirpation under global change scenarios. In addition to projected changes in August stream temperature and mean annual flow by 2080 (A), vulnerability is modeled as a function of decreased riparian cover (-50%; B), increased sedimentation (+50%; C), and increased nitrogen (+50%, D) relative to baseline levels. Sites modeled as suitable (i.e. where species presence is predicted) under baseline conditions are shown in all panels. No climate-induced extirpations are projected for rainbow trout in A. This is because occurrence probabilities exceed threshold levels for suitability and because stream temperatures for this subset of sites are projected to remain below thermal tolerance levels.



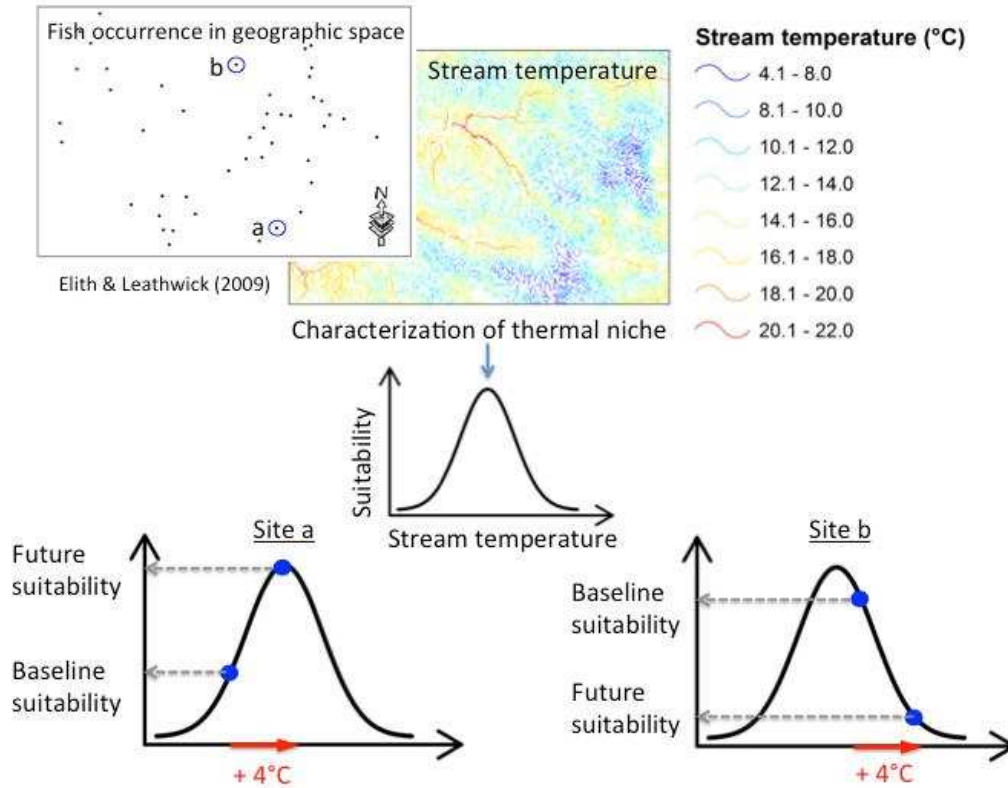


Figure A3 - 12. Thermal niches characterize suitability of stream temperature and can inform species' sensitivity to climate warming. Across their geographic range, species are expected to be differentially sensitive to a given degree of climate exposure, which can be understood as a function of the baseline temperature and of the response curve. A marginally suitable, cold site (a) becomes more suitable with a 4 °C increase in temperature whereas as a near optimal site (b) becomes unsuitable with the same degree of exposure.

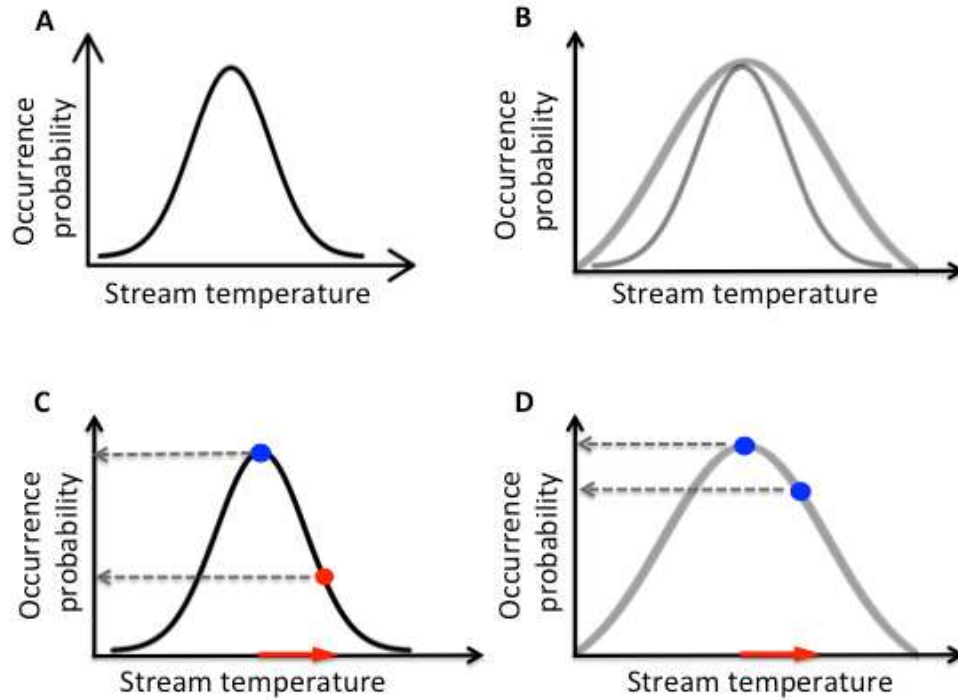


Figure A3 - 13. Thermal niches depict how species occurrence varies along a gradient of stream temperature (A). Differences in the characterization of thermal niches have important implications for species distribution modeling because niche breadth informs sensitivity of species to environmental change. Narrow thermal niches indicate that the range of temperatures considered suitable for a species is more restrictive than for a broad thermal niche (B). All other things being equal, sensitivity to warming can be considered a function of niche breadth and is useful for assessing climate vulnerability when combined with estimates of exposure. Warming-induced reductions in the probability of occurrence are likely to be greater under a narrow thermal niche (C) than for a broad thermal niche (D), given the same magnitude of exposure (red arrow indicating degree of warming), and may contribute to greater estimates of vulnerability due to more frequent classification of extirpations (red dot in C) versus persistence (blue dots).