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Synergistic effects of climate change and agricultural intensification on steelhead *Oncorhynchus mykiss* in the interior Columbia River basin

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ABSTRACT: Climate change is expected to have strong effects on river systems and their biota. It is unlikely that a changing climate will be the only stressor on river systems to increase in the future. Human population growth will necessitate increased resource use including agricultural intensification. Understanding how climate change will interact with agricultural intensification to affect river systems is important for effective management. We used a spatially explicit, habitat-based life cycle model, Ecosystem Diagnosis and Treatment (EDT), to examine the effects of climate change and agricultural intensification scenarios on the performance of steelhead *Oncorhynchus mykiss* in a Columbia River Subbasin. Climate change had strong negative impacts on basin-wide abundance, habitat capacity, productivity, and life-history diversity of steelhead, with the largest impacts under the most severe climate scenarios. Agricultural intensification also had strong negative effects on steelhead performance, particularly under the most severe scenario of complete removal of riparian buffers in crop production areas. When combined, both stressors had interactive effects on steelhead. The egg incubation stage was the most vulnerable to both stressors. Spawning adults were also strongly affected by climate change, whereas overwintering parr were affected by agricultural intensification. EDT modeling allowed an identification of areas within the subbasin most vulnerable to these stressors, as well as areas that are strongholds of productivity under future conditions. Finally, model results revealed that the most important areas to protect against both climate and agricultural change are not necessarily the same as those identified as high priority areas for protection and restoration under current conditions.

KEY WORDS: Habitat model · Downscaled climate change · Agriculture · Steelhead performance

1. INTRODUCTION

River systems are habitat for many ecologically, culturally, and economically important species (Postel & Richter 2003, Arthington et al. 2010). Rivers are particularly vulnerable to climate change as their dynamics are closely linked to water temperatures and discharge. Increased air temperature is expected to increase river temperatures, and changes in precipitation patterns may influence river discharge (Vörösmarty et al. 2000, Nohara et al. 2006, van Vliet et al. 2013). Warming temperatures and changing discharge patterns will create challenging conditions for many endemic species, particularly those adapted to cool water and specific discharge regimes, such as salmonids.

Pacific salmonids *Oncorhynchus* spp. are an important component of river ecosystems in the Pacific

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Northwest (PNW), USA, and Canada (National Research Council 1996), a region expected to be strongly influenced by climate change (Dalton et al. 2013). Many rivers in the region currently show warming trends associated with climate change (Arismendi et al. 2013). In addition, changes in precipitation patterns have measurably altered the hydrologic regime of streams in the PNW. Specifically, peak flow timing has changed and low-flow extremes have increased in duration and severity (Luce et al. 2014). Climate modeling indicates that increased river temperatures and precipitation changes will become more severe in the future (Mote & Salathè 2010, Beechie et al. 2013, DeBano et al. 2016a). The effect of these environmental changes on salmonids in the PNW is expected to be large, resulting in altered distributions, declines in abundance, and shifts in life history patterns (Crozier & Zabel 2006, Hague et al. 2011, Ruesch et al. 2012, Wade et al. 2013, Lawrence et al. 2014).

While climate change is predicted to have strong effects on salmonids in the PNW, it is unlikely to be the only factor that influences salmonid performance that will change in the future. A burgeoning human population will increase global demands for freshwater, food, and energy (Millennium Ecosystem Assessment 2005), including in the PNW. Increased demands for food must be met by an increase in agricultural production. Agriculture is a significant component of the economy in many areas of the PNW (United States Department of Agriculture 2010), and the need for increased production already drives land and water use policy in the region (Oregon Water Coalition [OWC] 2015). Agricultural production is likely to increase in the PNW even with the potential negative effects that climate change will have on crop production (Eigenbrode et al. 2013). One means of increasing crop production in a region is to convert currently uncultivated areas, such as riparian zones, into cropland. The conversion of existing riparian areas into cropland is possible under current rules governing streamside management of agricultural lands in Oregon, which do not require vegetative buffers (however, they do require some type of 'sediment retention structure,' Oregon Administrative Rules 603-095-0300; available at https://sos.oregon.gov/archives/pages/oregon_administrative_rules.aspx). Riparian vegetation buffers river systems from upland runoff, provides habitat for many aquatic species, stabilizes streambanks, and is a source of organic matter inputs that support river food webs (Gregory et al. 1991, Baxter et al. 2005). Thus, loss of riparian vegetation can have significant consequences for fish and other aquatic life (Pusey & Arthington 2003, Sievers et al. 2017). How agricultural intensification and other local stressors interact with climate change to influence ecosystems is not clear. Climate change effects could be extreme enough to 'swamp out' effects of local stressors or the combined effects of these stressors could be synergistic (Nelson et al. 2009, Ateweberhan et al. 2013, DeBano et al. 2016a).

Here we report the results of modeling work designed to examine the impacts of climate change, agricultural intensification through riparian vegetation loss, and the combination of these 2 stressors on the performance of steelhead *O. mykiss* in the Umatilla Subbasin of eastern Oregon. This current modeling effort is an extension of a previous study that examined effects of 3 climate change scenarios and 2 agricultural intensification scenarios on river habitat in this system (DeBano et al. 2016a). That work revealed that both stressors influenced the river environment: climate change through increased river temperatures and agricultural intensification through increased sediment input and decreased riparian function (DeBano et al. 2016a). It also revealed a spatial complementarity of the 2 stressors: climate change had a large effect on aquatic habitat in the upper basin while the effects of agricultural intensification were more prevalent in the lower and mid-basin (DeBano et al. 2016a).

While the effects of stressors on habitat conditions were apparent, it is less clear how these predicted changes in the river environment would affect steelhead. Steelhead use different parts of the watershed at different times of the year throughout their lifecycle, and each life stage is sensitive to a different range of characteristics. While climate change increased water temperatures in many areas, it was not clear if steelhead would experience significant exposure to these effects based on their spatio-temporal distribution during their life cycle. Given that steelhead mainly use the upper basin for spawning and rearing, it was also not clear whether agricultural intensification in the lower and mid-basin would influence their performance. To address these questions, we used a spatially explicit model to examine steelhead performance in the Umatilla Subbasin under the same set of climate change and agricultural intensification scenarios used in DeBano et al. (2016a). The spatially explicit nature of the model allowed an examination of changes in steelhead performance for the entire subbasin as well as specific areas within the subbasin. The objectives of this analysis were to: (1) examine the influence of each stressor individually as well as in combination on basin-wide abundance and habitat capacity of steelhead; (2) at a finer scale, identify which areas within the subbasin currently have the greatest steelhead performance and which are most vulnerable to climate change and agricultural intensification; (3) determine which life history stages are most vulnerable to the stressors; and (4) understand whether the spatial complementarity of the 2 stressors results in synergistic impacts on steelhead performance.

2. METHODS

2.1. The Umatilla Subbasin: present and future

The Umatilla Subbasin is a 5931 km^2 watershed located within Umatilla and Morrow Counties in northeastern Oregon (DeBano & Wooster 2004; our Fig. 1). The mainstem Umatilla River is 143 km, originating in the Blue Mountains at an elevation of 1768 m and emptying into the Columbia River at 79 m. The subbasin experiences strong seasonal fluctuations in both temperature and precipitation with warm days, cool nights, and little precipitation in the summer, and colder winters with average temperatures often only slightly above freezing. Most precipitation occurs during the fall, winter, and spring. The climate of the subbasin is also strongly influenced by elevation. Warm and dry conditions exist in the northwestern, low elevation portion of the subbasin, where precipitation falls mainly as rain (~12 cm annually). The high-elevation southeastern portion of the subbasin in the Blue Mountains is cooler and wetter, receiving an average of 140 cm of precipitation per year, primarily as snowfall.

Approximately 42% of the area in the subbasin is cropland, 42% is rangeland, 13% is forest, and 3% is urban. Agriculture is a major economic driver, with the 2 counties ranking second and third in farm sales in the state and gross farm and ranch sales exceeding $480 million annually (Oregon Department of Agriculture [ODA] 2014). Agricultural intensification is expected to occur in the Umatilla Sub-

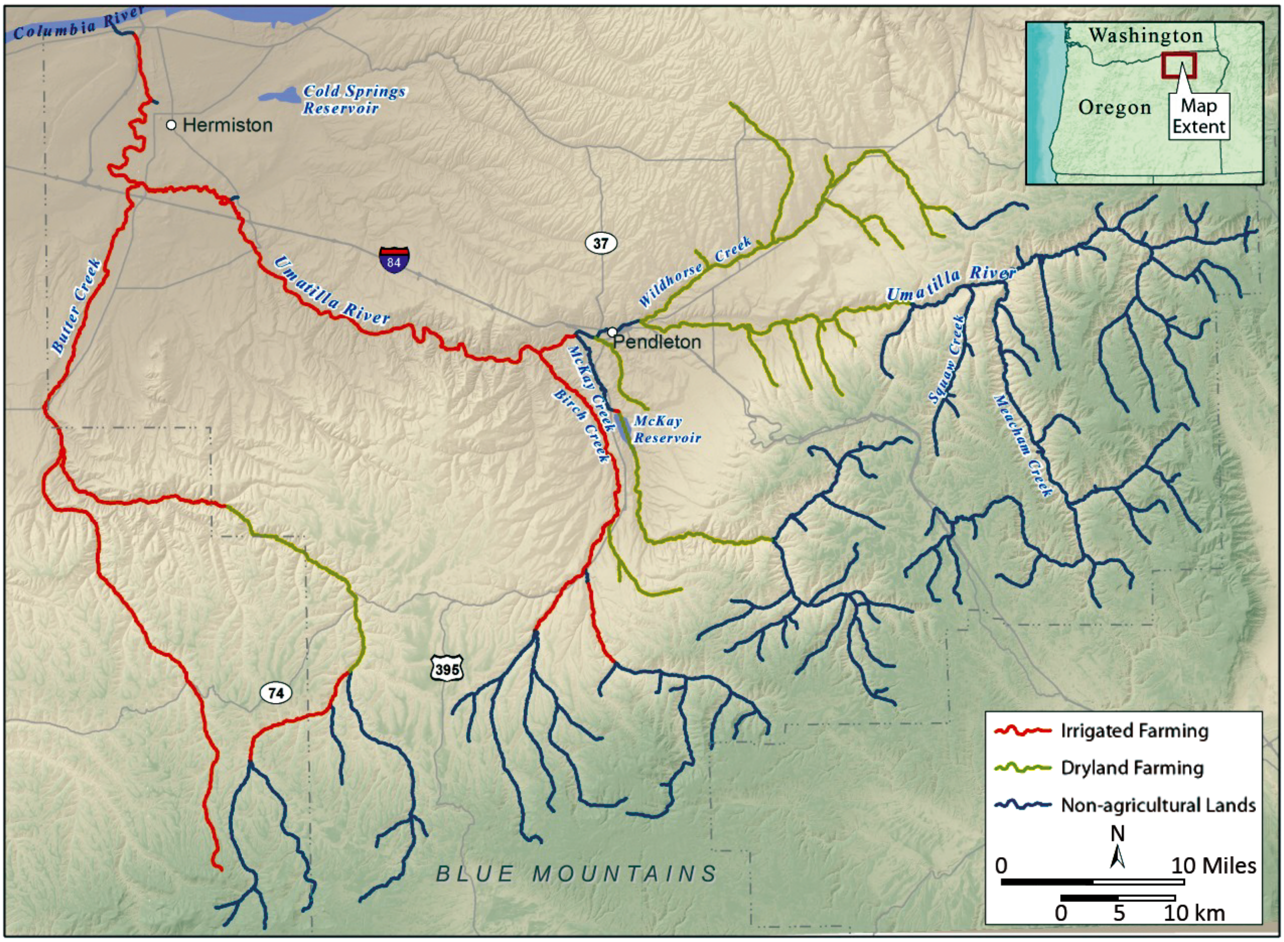

Fig. 1. Location of the Umatilla Subbasin in northeastern Oregon, USA and land uses associated with areas of the watershed

basin as a result of several recent developments (DeBano et al. 2016a). Water development projects funded by the Oregon Legislature will make more water available in the future for local growers, which will encourage the conversion of current dryland production and uncultivated areas to irrigated crop production (OWC 2015, Plaven 2015). Irrigated crops raised in the lower subbasin are more economically valuable than dryland crops of the upper subbasin (e.g. dryland wheat grown in the mid-subbasin markets for ~$200 to 400 per acre compared to over $10 000 per acre for irrigated crops such as watermelon; Connor et al. 2002, Galinato et al. 2014, ODA 2014). Increased water availability will incentivize expansion of irrigated agriculture into currently uncultivated areas, potentially leading agricultural producers to forego the development and maintenance of riparian buffers.

Historically, the Umatilla River supported populations of spring and fall Chinook salmon *Onchorhynchus tshawytscha*, steelhead *O. mykiss*, and Coho salmon *O. kisutsh*. With the advent of large-scale irrigated agriculture in the early 1900s, all native anadromous salmonids except for steelhead were extirpated from the subbasin (Phillips et al. 2000). A series of large water exchanges and restoration projects in the 1980s and 1990s improved river conditions sufficiently to support the reintroduction of Chinook and Coho (Phillips et al. 2000). All salmonid stocks in the Umatilla Subbasin are currently supplemented with hatchery production. While prior and ongoing habitat restoration efforts have yielded significant habitat benefits, the aquatic ecosystem in the Umatilla and the salmonid species it supports are still at risk. Steelhead of the Umatilla River were federally listed as threatened in 1998 (Umatilla River steelhead are a population of the Middle Columbia River evolutionarily significant unit [ESU]). While the lower river no longer completely dries during the irrigation season, up to 99% of streamflow is diverted for irrigated agriculture and other uses in summer (Miller et al. 2007). The resulting loss in habitat and increased water temperature associated with water withdrawal have made the lower river unsuitable habitat for juvenile salmonids, and have negatively affected the entire aquatic community (Miller et al. 2007, Brown et al. 2012, Wooster et al. 2016). The condition of riverine and riparian habitat in the Umatilla Subbasin is expected to deteriorate further with climate change, with the effects of decreased stream flow and increased water temperature expanding throughout the mainstem Umatilla River and into its tributaries (DeBano et al. 2016a).

Umatilla steelhead are of particular interest because the population has persisted despite the long history of habitat degradation in the subbasin. Steelhead are an anadromous form of rainbow trout with 2 primary life history forms: winter-run fish that reenter natal streams in a mature state and spawn shortly thereafter in winter and spring; and summer-run fish that return in an immature state in the summer and fall, overwinter as they mature, and spawn the following spring. All steelhead in the Umatilla River and interior Columbia Basin are summer-run. Summer-run steelhead demonstrate considerable life history diversity (summarized in Leider et al. 1986, Washington Department of Fish and Wildlife & Oregon Department of Fish and Wildlife 2002). Adults spend 1 to 3 yr in the ocean and then enter their natal rivers from March through October. Spawning occurs from January to June. Juveniles generally spend 1 to 2 yr in freshwater before they smolt and outmigrate in May and June. In addition, steelhead also demonstrate the ability to revert to a resident life history form when the ocean is inaccessible (Narum et al. 2004). This flexible life history provides steelhead with a high level of adaptive capacity relative to other salmonids with a more rigid life history.

2.2. Modeling steelhead responses to climate change and agricultural intensification

Because of its threatened status and importance to the economy and culture of the region, we simulated responses of Umatilla River subbasin steelhead to changes in environmental attributes expected to result from climate change and agricultural intensification. Specifically, we examined how 3 climate change scenarios (high, moderate, and low) and 2 agricultural intensification scenarios (extreme and moderate), and their interaction affected steelhead equilibrium abundance, habitat capacity, productivity, and life history diversity compared to current conditions. To do so, we used the Ecosystem Diagnosis and Treatment (EDT) model.

EDT is a habitat-based life cycle model that characterizes the aquatic environment temporally and spatially 'through the eyes of the fish'. EDT was developed in the mid-1990s by a team of fisheries biologists and mathematicians who recognized that multiple listings of PNW salmon and steelhead under the Endangered Species Act (ESA) would create complex resource management challenges (Lichatowich et al. 1995). This created the need for a disciplined method for prioritizing habitat protection

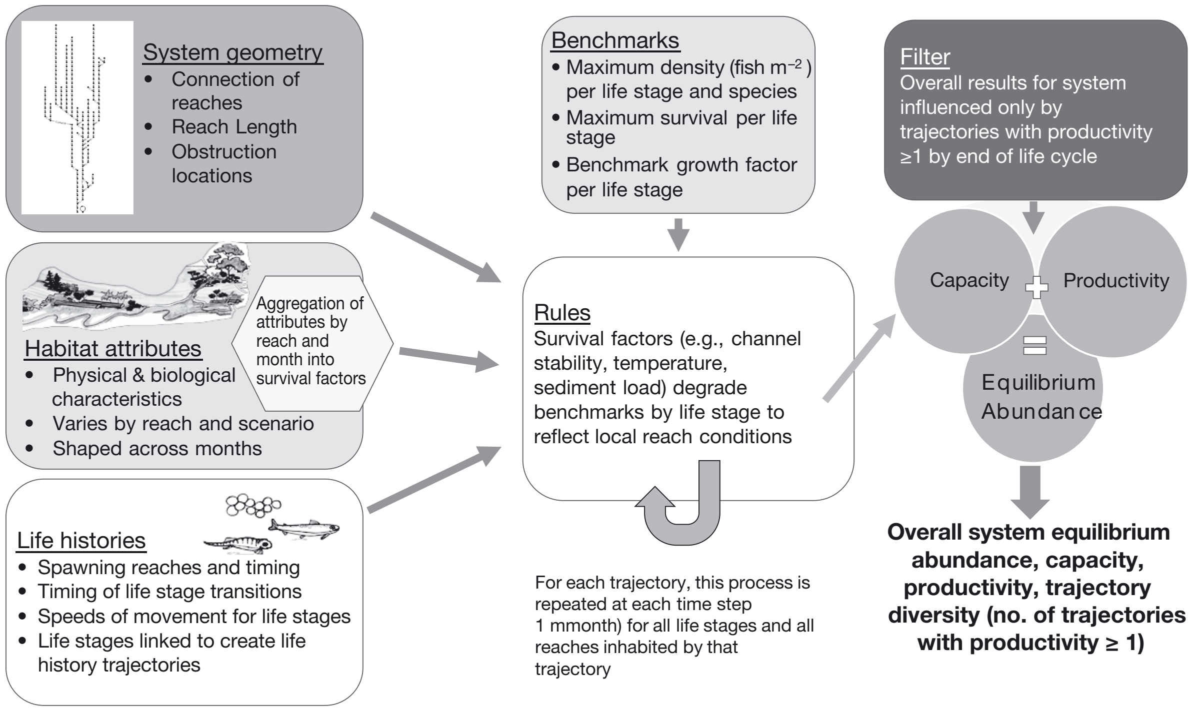

Fig. 2. Flowchart outlining the steps in Ecosystem Diagnosis and Treatment (EDT) modeling. System geometry, habitat attributes, and general life histories are input parameters. EDT combines these parameters and uses a set of 'Rules' that characterize how the input parameters interact to lower salmonid capacity and productivity below benchmark values. For each life history trajectory, this process is iterated across all life stages to produce a productivity value. Only trajectories with productivity values ≥1 are used to determine population-level capacity, productivity, and equilibrium abundance

and restoration needs, and identifying data gaps (Mobrand et al. 1997, Lestelle at al. 2004). EDT has proven to be a powerful tool for salmon habitat analysis. The approach has been applied to over 10 000 reaches in 122 watersheds in the PNW (Blair et al. 2009), including the Umatilla Subbasin (DeBano & Wooster 2004) and most of the other 58 subbasins involved in planning efforts for the Northwest Power and Conservation Council (NWPCC 2005). The model platform is available to the public (https://ecosystems.azurewebsites.net/Applications/EDT/).

EDT is a reach-based model, composed of a model watershed, a migratory corridor (e.g. the Columbia River), and ocean habitat. EDT results can be reported by reach and for the entire population. EDT calculates Beverton-Holt productivity, capacity and equilibrium abundance, and an index of life history diversity for the model population. These outputs are analogs to the Viable Salmonid Population (VSP) parameters developed by the National Marine Fisheries Service to support recovery of ESA-listed species (McElhany et al. 2000). A flowchart illustrating the EDT model is shown in Fig. 2.

The Beverton-Holt stock recruitment function (Beverton & Holt 1957) is the computational foundation of EDT. The developers selected Beverton-Holt because it has tractable mathematical properties and provides a useful framework for quantifying fisheries population dynamics based on habitat condition (Moussalli & Hilborn 1986, Hilborn & Walters 1992). The function has 2 input parameters, density-independent survival (or productivity) and the asymptotic carrying capacity (Blair et al. 2009). These parameters are directly related to the quality and quantity of habitat, respectively (Hayes et al. 1996). The Beverton-Holt function has recursive properties (Moussalli & Hilborn 1986), making it possible to disaggregate habitat productivity and capacity by life stage and location.

In general, a typical EDT model analysis involves 4 components (as described in Blair et al. 2009, Steel et al. 2009): (1) defining the model habitat environment as a reach network and using up to 46 different environmental attributes (e.g. flow metrics, temperature) to describe habitat conditions under a set of alternative habitat scenarios by reach and month; (2) defining a model fish population and generating a life stage-specific dispersal model called a trajectory set, composed of thousands of individual trajectories; (3) calculating the productivity and capacity of each trajectory under each habitat scenario using species and life stage-specific rules; and (4) combining trajectory performance to calculate population level metrics for each habitat scenario and running a splice analysis to identify reach-level habitat protection and restoration priorities.

The life history trajectory set is a core component of every EDT model analysis. The EDT Trajectory Generator is a dispersal model that builds a set of randomly generated life history pathways, or trajectories, through the model habitat environment using a set of user-defined population parameters and life stage constraints. Population parameters include age structure, behavioral strategies (e.g. stayer versus mover rearing behavior), sex ratio, and fecundity. Life stage constraints include spawn timing, time periods and locations where transitions between life stages can occur, and movement speed during each life stage. Constraints are expressed as ranges, allowing the user to set bounds on the spatial and temporal expression of each life stage.

Trajectories do not represent individual fish. They are a subsample of the watershed habitat that the target species could use to complete a specific life history strategy. The Trajectory Generator builds each trajectory by selecting an age class and behavioral type from the user-defined population structure (e.g. a mover-type steelhead that smolts at age-2 and spends 1 yr in the ocean), and randomly selecting timing, speed, location, and duration values for each of the component life stages from the available constraint ranges.

The randomly selected constraint values for each trajectory are used to generate a unique spatio-temporal pathway through the model environment. For example, hypothetical steelhead trajectory no. 1 might initiate (spawn) in Umatilla River reach X on April 6, incubate for 67 d, rear in freshwater for 2 yr in close proximity to its natal reach, begin outmigration on May 17, enter the ocean on June 28 and reside there for 1 yr, reenter the Umatilla Subbasin on September 12, and hold for 206 d before spawning. Each trajectory represents a distinct life history strategy and experiences different environmental exposure. A typical trajectory set is composed of thousands of trajectories, which collectively provide a useful representation of the range of potential life history expression for the modeled population. An appropriately defined trajectory set is capable of representing a diverse array of age classes and life history strategies, providing a mechanism to consider potential evolutionary adaptation to changing habitat conditions.

Each trajectory is recorded in EDT as a series of sequences, with each sequence representing a specific life stage and reach during a given month on an instantaneous time step. Transition to a new reach, the next life stage, or the next month creates a new sequence record. All trajectories complete their respective life cycles, traveling from their spawning reach to the ocean and back following the itinerary determined by their specific life stage constraints.

EDT calculates productivity and capacity of each trajectory sequence using benchmarks and habitat rules (Fig. 2). Benchmarks are species-specific duration, survival and density values for each life stage in different environment types (e.g. small tributary, large river mainstem) under idealized habitat conditions. The benchmarks set the baseline for calculating the habitat capacity and productivity for each habitat scenario. The habitat rules are life stage-specific sensitivity curves for each environmental attribute (e.g. incubation sensitivity to substrate fines) that degrade sequence productivity and capacity from benchmark, based on the combination of habitat attributes present and duration of exposure. EDT calculates productivity, capacity, and survival individually and cumulatively for each trajectory sequence. The model integrates the performance of all trajectories to calculate the population productivity, capacity, and equilibrium abundance across different spatial scales (e.g. reach and subbasin).

The EDT life history diversity metric is based on the proportion of trajectories originating from a selected reach that 'succeed' or 'fail.' A trajectory may succeed or fail under each modeled habitat scenario based on the conditions it experiences on its unique spatio-temporal pathway. A 'successful' trajectory completes its life cycle with a cumulative productivity equal to or greater than 1 (i.e. at least 1 returning adult for every spawner). The number of trajectories from a selected spatial unit that succeed provides an index of life history diversity that those habitat conditions can support considering the watershed environment as a whole. However, trajectory diversity is influenced by reach length with longer reaches having more trajectories. Therefore, we compared trajectory diversity among reaches and scenarios as trajectory diversity per km of reach.

At the entire basin scale, the impact of the climate change and agricultural intensification scenarios was evaluated by applying each scenario (including current conditions) to the entire basin and then comparing habitat capacity, equilibrium abundance, productivity, and trajectory diversity among the different scenarios. The last 2 metrics were compared using measures of central tendency for all reaches. At the reach level we compared different scenarios by mapping productivity and trajectory diversity for

Table 1. Survival factors and environmental attributes used to examine the impact of climate change, agricultural intensification, and both stressors simultaneously on the performance of steelhead *Oncorhynchus mykiss*. Environmental attributes were used to describe current conditions in the Umatilla Subbasin and conditions under different climate and agricultural intensification scenarios (see DeBano et al. 2016a for details on estimating values for each attribute). Environmental attributes are aggregated into 'survival factors' that characterize changes in the environment to steelhead performance. An 'x' in the column indicates that the environmental attribute was included in the climate change, agricultural intensification, or both stressors combined ('Both') scenario development

Survival factor	Environmental attribute and brief description	Climate change	Agricultural intensification	Both
Oxygen	Dissolved oxygen — average dissolved oxygen within the water column		x	
Sediment load	Embeddedness — extent that larger cobbles or gravel are surrounded by or covered by fine sediment		x	
	Fine sediment — % substrate comprised of fine sediment.		x	
	Turbidity—the severity of suspended sediment episodes within the stream reach		x	
Flow	Low flow—average daily flow during the normal low flow period	x		
Toxins	Metals/pollutants in sediments/soils—the extent of heavy metals and other toxic pollutants within the stream sediment and/or soils adjacent to the stream channel		x	
	Miscellaneous toxic pollutants — the extent of miscellaneous toxic pollutants in the water column		x	
Habitat diversity; channel stability	Riparian function—intactness of stream and floodplain linkages		x	
	Wood—the amount of large woody debris within the reach		x	
Temperature	Summer water temperature—a function of the maximum			x

all 44 reaches. Our measure of median productivity is based on successful trajectories (i.e. productivity ≥ 1) only.

Finally, EDT can determine reaches that provide the greatest improvement in steelhead performance if those reaches are restored or protected. EDT calculates these reach-level benefits by running the same trajectory set through different habitat scenarios (McElhany et al. 2010). In a 'typical' analysis (e.g. those analyses conducted for the 2004 subbasin planning process), EDT uses current conditions and historical ideal conditions as the 2 scenarios to compare fish performance. Current conditions are applied to the entire watershed and then the model identifies priority reaches by systematically 'splicing,' or replacing, current conditions with historic conditions on a reach-by-reach, limiting factor-by-limiting factor basis and evaluates how that change affects productivity, capacity, equilibrium abundance, and diversity of all trajectories at each spatial scale. The highest-priority areas for restoration or protection are those reaches that produce the greatest improvement in population performance.

For our current work, we conducted a slightly different splice analysis. Priority reaches for protection under current conditions were identified by applying each of the climate change and agricultural intensification scenarios across the entire basin and then splicing in current conditions on a reach-by-reach basis. Priority reaches for protection in each future conditions are those that generate the greatest improvement in steelhead performance (measured here as basin-wide equilibrium abundance) if they can be protected and maintained in their current state given future climate change and/or agricultural intensification. Because funding is often limited for river restoration and protection and decisions need to be made regarding how limited funds are spent, we compared priority reaches for protection identified in the current EDT analysis to those reaches identified as priority reaches for restoration under the 2004 EDT work (DeBano & Wooster 2004) to determine if, in general, they are the same reaches.

2.3. Environmental attributes examined

The Umatilla EDT model developed for the 2004 subbasin planning effort is structured on a reach network with 2 primary components, the Umatilla Subbasin composed of 44 reaches and the Columbia River migration corridor and Pacific Ocean. Decisions on values of environmental attributes for each reach were made based on available data and consensus of professional judgment when suitable data were lacking (described in DeBano & Wooster 2004).

To examine different scenarios of climate change and agricultural intensification, as well as their interaction, we varied 10 EDT environmental attributes that we believed would be most strongly affected by climate change and agricultural intensification (DeBano et al. 2016a). Attributes are rated on a scale from 0 to 4 and are briefly described in Table 1. More descriptions of attributes can be found in Lestelle et al. (2004), Lestelle (2005), and DeBano et al. (2016a). We quantified reach specific values for each attribute in Table 1 for current conditions and future scenarios (described in detail in DeBano et al. 2016a,b). Environmental attributes are aggregated into 'survival factors' that relate changes in the environment to steelhead productivity (Lestelle 2005; our Table 1). The Columbia River mainstem and Pacific Ocean component of the model are parameterized to represent existing habitat conditions in the early 2000s. We applied the same Columbia River and ocean survival conditions for each scenario to avoid the confounding effects of out-of-basin survival on model results.

2.4. Developing climate scenarios

We developed 6 climate change scenarios and focused on the effects of climate change on low flows and maximum summer water temperature (Table 1). We chose low flow to be a primary hydrological variable of interest because, in much of the western USA, low flows are limiting for salmonids and many other forms of aquatic life (Harvey et al. 2006). Although increases in winter and spring flooding events are also an important factor influencing salmonids (Mantua et al. 2010), we chose to focus on summer flow because of its current limiting role in the subbasin (DeBano & Wooster 2004). For stream temperatures, the EDT ranking system takes into account both the mean maximum daily temperature and the number of days above certain threshold temperatures (DeBano et al. 2016a, their Appendix 2). Salmonids are not only sensitive to temperature extremes, but also the length of time those extremes are encountered. Prolonged exposure to temperatures above this threshold can lead to higher mortality, faster growth rates, altered life histories, and smaller sizes (Richter & Kolmes 2005).

We characterized low flow using the Western US Stream Flow Metric Dataset to predict mean summer flow for current and future climate scenarios (DeBano et al. 2016a). Flow values were generated using the Variable Infiltration Capacity (VIC) macroscale hydrologic model (www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml; Wenger et al. 2010). We used data from 1978 to 1997 to represent current conditions and 6 climate change scenarios. Two moderate scenarios (referred to hereafter as 'Mod 2040' and 'Mod 2080') were based on a 10 model ensemble mean for 2040 and 2080 (IPCC 2007). One of the ensemble models (MIROC.3.2) projects warmer and drier conditions for the PNW, and was used to model severe climate conditions (referred to hereafter as 'High 2040' and 'High 2080'). Finally, another ensemble model (PCM1) projects less severe climate change for the PNW, with cooler and wetter summers than the ensemble mean, and thus was used to model less severe climate change (referred to hereafter as 'Low 2040' and 'Low 2080'). Low flow estimates were converted to ranked EDT attributes by calculating the percent reduction of flow from current conditions (see DeBano et al. 2016a for more details).

We estimated maximum summer water temperatures for each reach by developing a multiple regression model based on 4 independent variables: air temperature, radiation, flow, and elevation (described in DeBano et al. 2016a,b). Maximum water temperature ranks were established based on an algorithm that takes into account the maximum daily temperature, as well as the duration of temperatures above certain thresholds during July and August for all years for which data were available (see DeBano et al. 2016a). Values for reach-specific independent variables used in the temperature regression were determined both for current conditions (for developing the model) and for future conditions (for predicting water temperature under future scenarios). Downscaled air temperatures for the Umatilla Subbasin were obtained from the University of Idaho (http://climate.northwestknowledge.net/MACA/) through their Multivariate Adaptive Constructed Analogs (MACA) Statistical Downscaling Method project (Abatzoglou & Brown 2012). Because the MACA models and their method of incorporating emission scenarios are different than those used for the VIC modeling, we used the visualization tool on the MACA website to select 3 models that give low (inmcm4), medium (bcc-csm1-1), and high (Had GEM2-CC) temperature predictions for our region. Data for the high emission scenario (RCP8.5), which represents a future with no climate action and high emissions, was used. Current conditions were characterized using 'historical data' generated with the moderate GCM (bcc-csm1-1) as a monthly average. For the water temperature multiple regression, mean monthly daily maximum air temperatures for July were used: the mean for 1985–2005 was used to describe current conditions, the mean from 2030–2050 was used to describe 2040 conditions, and the mean from 2070–2090 was used to describe 2080 conditions.

2.5. Developing agricultural intensification scenarios

We examined steelhead responses to 2 future agricultural scenarios. One, which we term the 100% Removal scenario, was designed to investigate what we consider to be the most extreme agricultural intensification scenario that could impact riparian areas in the Umatilla Subbasin. In this scenario, increased value of agricultural commodities results in all uncultivated areas in currently farmed lands, including woody and herbaceous riparian buffers, becoming cultivated. We limited the conversion of riparian areas to currently farmed areas (Fig. 1) because the primary reasons why certain areas are not cultivated in the subbasin relate to a combination of low rainfall, the expense of transporting water to the area, topography, soil depth, and landownership (e.g. federal, state, and tribal lands). These factors make it unlikely that many areas in the upper watershed would be cultivated, even with increased crop values.

We also modeled a less extreme scenario of agricultural intensification, the 75% Removal scenario. In this scenario, increasing value of agricultural commodities provides an incentive for farmers to convert 75% of their existing riparian buffers to cropland. This reduction is incorporated into the model as a change of buffer width, rather than length, because of the difficulty of cultivating land at the very edge of the stream. As with the 100% Removal scenario, the reduction in buffer width only occurs on land currently farmed.

We examined 9 attributes related to agricultural intensification (Table 1): riparian function, woody debris, embeddedness, fine sediment, maximum summer water temperature, dissolved oxygen, metals and pollutants in sediments and soils, miscellaneous toxic pollutants in the water column, and turbidity. Current and future values for these attributes were estimated in DeBano et al. (2016a). In general, our approach was to change riparian function relative to the 2 agricultural intensification scenarios, and then estimate the effect of those changes on the other 8 attributes. In the 100% Removal scenario, we assumed that the conversion of all riparian buffers to cropland would result in all current riparian function being lost in agricultural areas, so all riparian function values were changed to the worst case rank of '4' for reaches located in agricultural areas (Lestelle 2005). For the 75% Removal scenario, we decreased riparian function by increasing the current riparian function values by 1 rank (Lestelle 2005). Any values greater than 4 were truncated to 4.

We expected maximum water temperatures to increase under the 100% Removal scenario because the removal of all riparian vegetation would result in the loss of woody vegetation in riparian areas that currently shade streams. Increases in solar radiation should lead to increased water temperature. To estimate changes in water temperatures, we used the same multiple regression model described in the climate change scenario section, but changed the solar radiation term through manipulation of shade for the 100% Removal scenario only. Water temperature was not changed for the 75% Removal scenario because only buffer width was reduced (not length), so that 25% of the current buffers closest to the stream (and providing the shading effect) remained intact. More details, including how we estimated the effect of reduced riparian function on the other 7 attributes, can be found in DeBano et al. (2016a).

2.6. Interaction scenarios

We examined 4 climate change × agricultural intensification interaction scenarios: Low 2080 × 75% Removal, High 2080 × 75% Removal, Low 2080 × 100% Removal, and High 2080 × 100% Removal. In the 2 climate change × 100% Removal interaction scenarios, water temperature was impacted by changes in both radiation and air temperature. We used the multiple regression model described above to estimate the effect that changes in radiation and air temperature had on water temperature ranks. For interactions involving the 75% Removal scenario, water temperatures took on the values associated with the interacting climate change scenario since there was no loss of stream shading in the 75% Removal scenario, and therefore no changes in solar radiation input. Current and future values for attributes used in all scenarios are available online (https://doi.org/10.5061/dryad.564q7; DeBano et al. 2016b).

2.7. Current diversity versus future productivity

We also examined the relationship between current life history diversity and future productivity at the reach level. Life history diversity is predicted to increase the probability of survival of species under environmental changes (Fox 2005, Greene et al. 2010). EDT output allowed an examination of this at the small, reach scale. We predicted that current reach-level diversity would be higher in reaches that maintain productivity under the most extreme future scenario (High 2080 × 100% Removal) than in reaches in which steelhead productivity is lost in that scenario. This prediction was examined using Welch's 2 sample *t*-tests in R (version 3.4.0, R Core Team 2017).

2.8. Model runs

We ran EDT with updated climate and/or agricultural intensification attributes for current conditions and the 12 future scenarios (6 climate change, 2 agricultural intensification, and 4 interaction). Output included basin-wide abundance and habitat capacity under future scenarios; productivity and trajectory diversity (scaled to reach length) at the reach level under future scenarios; identification of sensitive life stages and environmental attributes contributing to observed effects; and identification of reaches most important for protection in future scenarios. Individual reach-level results were mapped using ArcGIS 10.1.

3. RESULTS

3.1. Basin-wide and reach-level trends

EDT estimates a single basin-wide value for equilibrium abundance and capacity. Both variables decreased in all future scenarios compared to current conditions, with more severe climate scenarios showing larger declines than moderate or low scenarios, and with 2080 scenarios leading to larger decreases than 2040 scenarios (Fig. 3a,b, Table 2). Steelhead abundance decreased by 25 to 37% relative to current conditions for 2080 scenarios and by 8 to 16% for 2040 scenarios. Capacity decreased by 12 to 16% relative to current conditions for 2080 scenarios and by 6 to 9% for 2040 scenarios. Losses associated with agricultural intensification scenarios were not as pronounced, but followed the same pattern of increased loss with increased disturbance, with

Table 2. Percentage loss in equilibrium abundance and capacity for each scenario relative to current conditions. Removal: uncultivated areas in farmed lands becoming cultivated

Scenario type	Scenario	% Lost Abundance	% Lost Capacity
Climate change	Low 2040	8.5	6.1
	Mid 2040	12.9	7.4
	High 2040	16.5	8.8
	Low 2080	24.7	11.8
	Mid 2080	30.4	13.1
	High 2080	36.8	16.0
Agricultural intensification	75% Removal	11.5	10.9
	100% Removal	27.3	26.9
Combined	Low 2080 × 75% Removal	33.6	22.0
	Low 2080 × 100% Removal	45.1	36.0
	High 2080 × 75% Removal	46.2	25.8
	High 2080 × 100% Removal	56.5	39.0

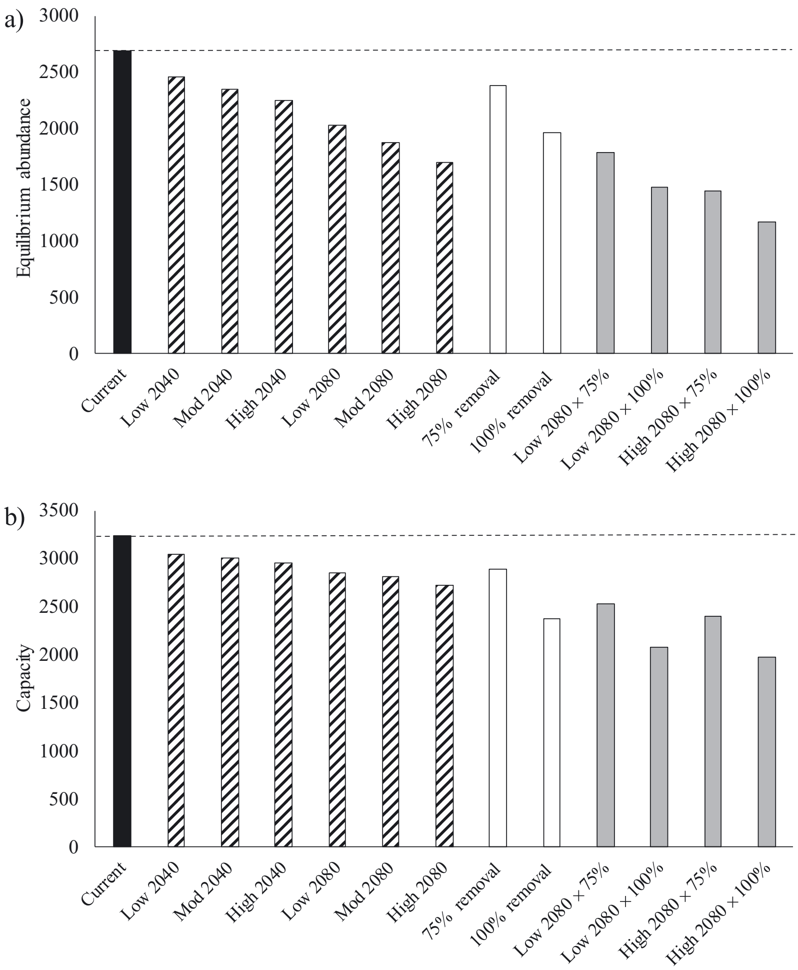

Fig. 3. Basin-wide responses of steelhead *Oncorhynchus mykiss* (a) equilibrium abundance and (b) habitat capacity to current conditions (black bar), climate change scenarios (striped bars), agricultural intensification (open bars), and climate change and agricultural intensification (gray bars). Removal: uncultivated riparian areas in farmed lands becoming cultivated. The dashed horizontal line indicates performance under current conditions

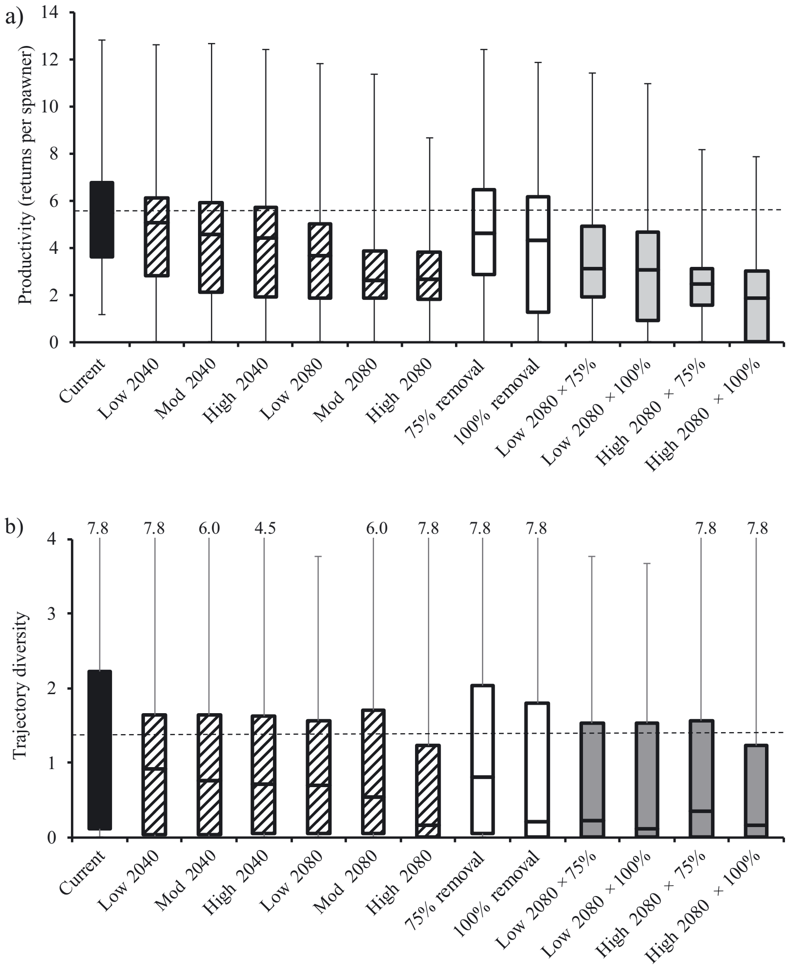

Fig. 4. (a) Productivity and (b) trajectory diversity for current conditions and the 12 future scenarios. Box and whisker plots show the medians (horizontal lines), the 2 inner quartiles (boxes), and the range of values summarized across all reaches that had at least 1 successful trajectory under current conditions. The dashed horizontal line is the median value for current conditions. For clarity of presentation in (b), the maximum values are provided for scenarios with maximum values >4.0. Current conditions (black boxes), climate change (striped boxes), agricultural intensification (clear boxes), and combined scenarios (gray boxes)

the 75% Removal scenario resulting in an 11% decrease in abundance and capacity compared to current conditions and the 100% Removal scenario resulting in a 27% decrease in both variables (Fig. 3a,b, Table 2). Both disturbances together resulted in the greatest losses in abundance and capacity relative to current conditions than either disturbance alone (Fig. 3a,b, Table 2). In the worst-case scenario (High 2080 × 100% Removal), basin-wide abundance decreased by 56% and capacity decreased by 39%.

EDT generated 5704 steelhead trajectories over the entire subbasin. The great majority of these were unsuccessful (i.e. productivity <1.0); for example, under current conditions only 20.6% of all trajectories were successful. Productivity of successful trajectories and the number of successful trajectories were generated for each reach, and central tendencies are summarized for each scenario (Fig. 4a,b). Both variables responded negatively to climate change, agricultural intensification, and their interaction in much the same way as abundance and capacity. The High 2080 × 100% Removal scenario resulted in the lowest productivity (Fig. 4a). The lowest median trajectory diversity values were generated by the High 2080, 100% Removal, Low 2080 × 100% Removal, and High 2080 × 100% Removal scenarios (Fig. 4b).

Mapping illustrated reaches with the greatest productivity and trajectory diversity under both current conditions and future scenarios (Figs. 5 & 6). Although several strongholds of productivity and diversity persist under most scenarios, many highly productive and/or diverse reaches were lost under the most extreme scenarios (Figs. 5 & 6). In fact, under the range of scenarios, the number of highly productive (≥5 returns per spawner) and diverse (≥2 trajectories km^{-1}) stream kilometers decreased by 12 to 92% and 16 to 71%, respectively, with interactive scenarios resulting in the highest losses (Table 3).

3.2. Life stages affected and underlying environmental drivers

The impact of future scenarios on specific steelhead life stages, measured by the percent decline in performance of the stage relative to current conditions, varied depending on the disturbance (Table 4). The egg incubation stage was the most sensitive for all scenarios examined (with the exception of the 75% Removal Scenario) (Table 4). Spawning was the second most vulnerable stage for climate change and most interaction scenarios (Table 4). In contrast, overwintering parr in their first year was the second most vulnerable stage for the agricultural intensification scenarios (Table 4).

The survival factors contributing most to observed effects also varied by scenario. Temperature was the only survival factor with moderate to high impacts on steelhead under climate change scenarios (Table 5).

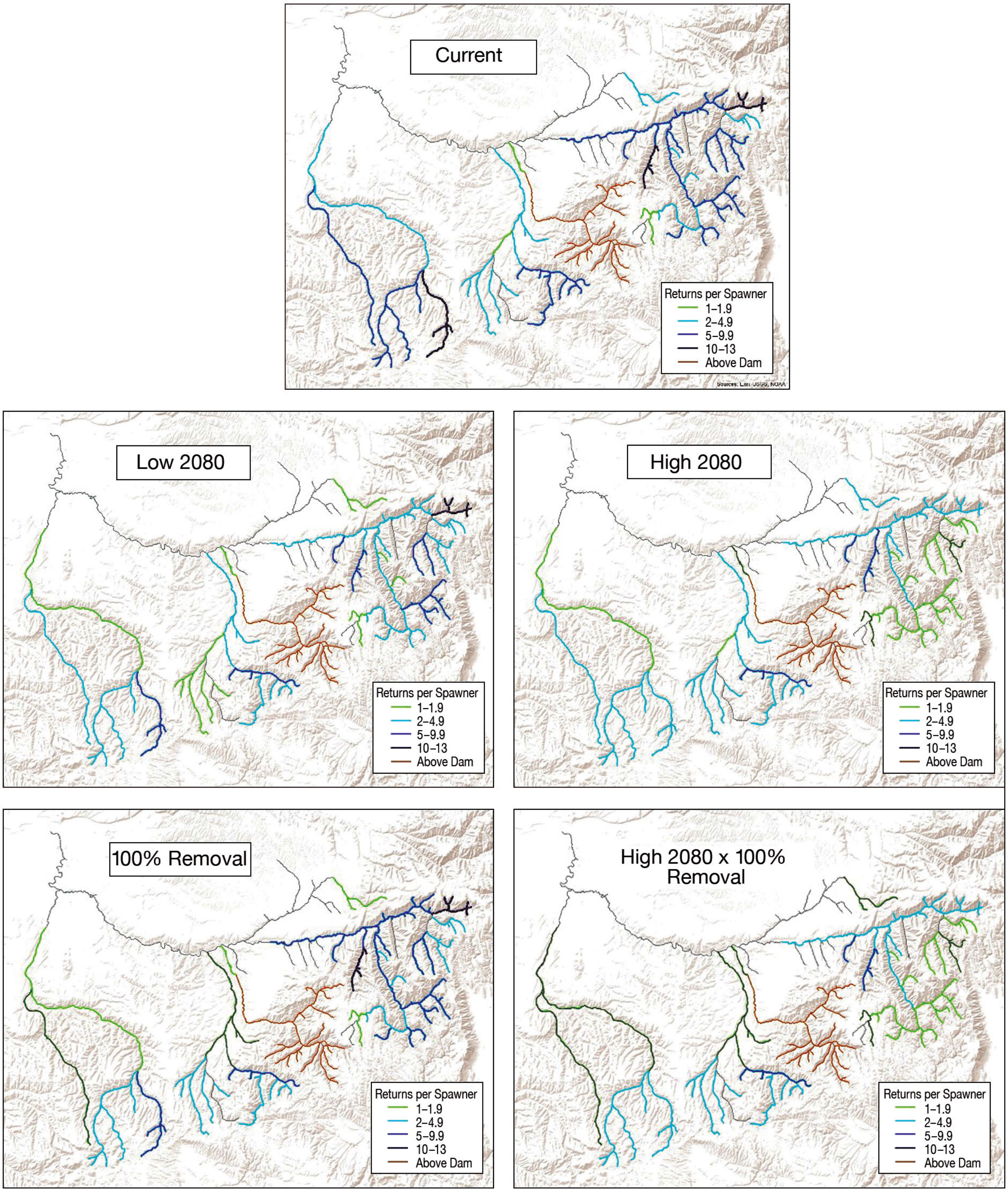

Fig. 5. Average productivity (returns per spawner) for all successful trajectories in each reach for current conditions and 4 scenarios. Gray lines indicate reaches with no successful spawning

Agricultural intensification scenarios influenced steelhead through more environmental pathways than climate change (Table 5). For the 75% Removal scenario, sediment load was the most important survival factor, and for the 100% Removal scenario channel stability and habitat diversity combined with sediment load to negatively impact steelhead (Table 5). Important survival factors in the interactive scenarios were generally combinations of the factors found for each stressor independently (Table 5).

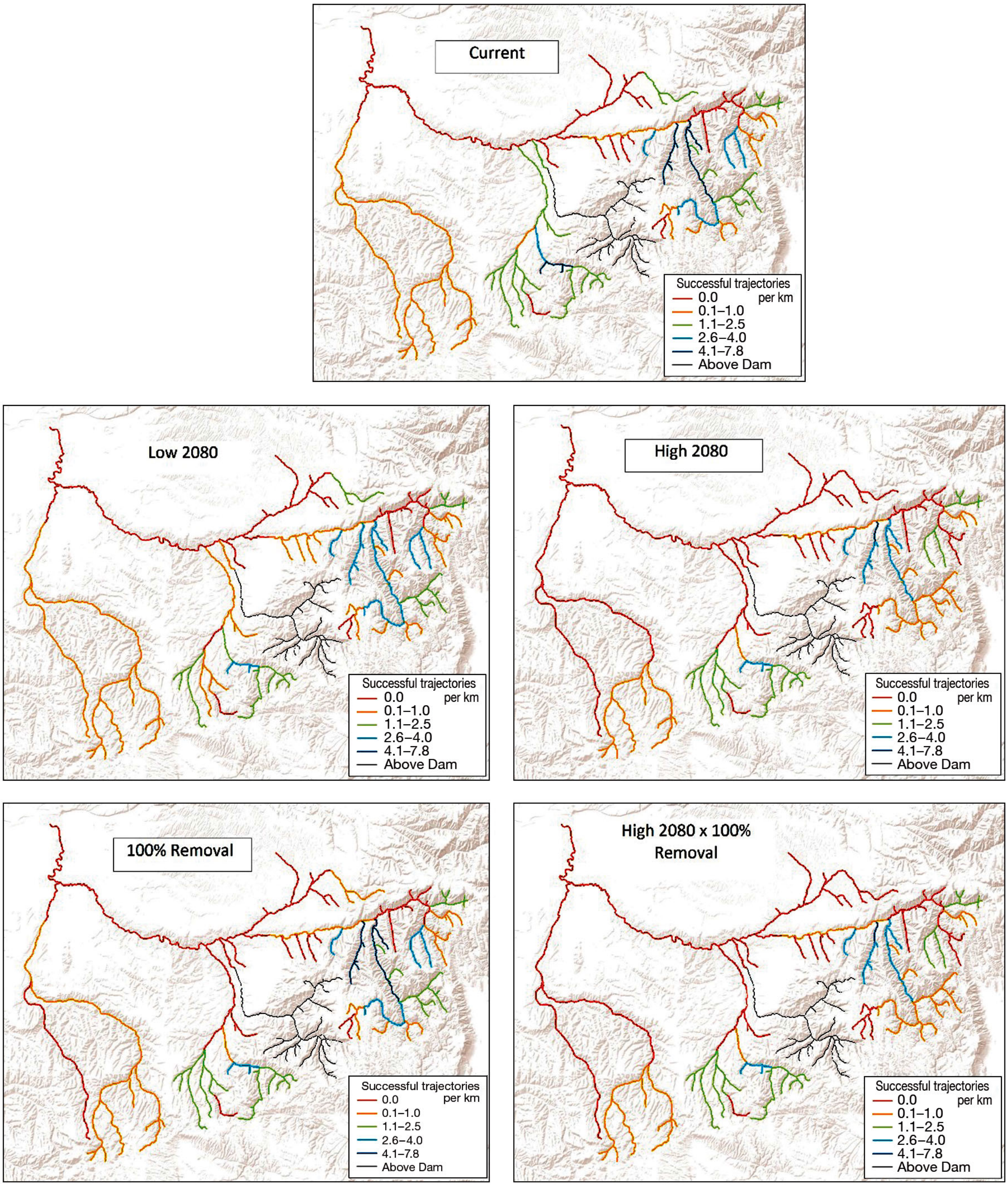

Fig. 6. Trajectory diversity (i.e. number of successful pathways) in each reach for current conditions and 4 future scenarios

3.3. Preservation and restoration under changing climate and expanding agriculture

For future scenarios, the EDT splice analysis determined which reaches would provide the greatest gain in steelhead numbers if they were protected from effects of climate change and agricultural intensification (Fig. 7). For current conditions, the splice analysis revealed the reaches that would provide the greatest gains in steelhead numbers if restored to historical conditions. As Fig. 7 shows, these reaches are found largely in the lower and mid-subbasin. Priority reaches for protection from future agricultural intensification (as a sole stressor) are also primarily in the lower and mid-subbasin (Fig. 7). In contrast, reaches providing the greatest gains in steelhead

Table 3. The number of stream kilometers that are highly productive (≥5 returns per spawner) and diverse (≥2 trajectories km^{-1}) under current conditions and future scenarios, and the percent reduction in productivity and diversity in future scenarios relative to current conditions

Scenario type	Scenario	Productivity km	Productivity % Reduction	Diversity km	Diversity % Reduction
Current		431		256	
Climate change	Low 2040	379	12	216	16
	Mod 2040	374	13	216	16
	High 2040	325	25	183	28
	Low 2080	145	66	148	42
	Mod 2080	55	87	149	42
	High 2080	41	91	73	71
Agricultural intensification	75% Removal	260	40	191	25
	100% Removal	228	47	181	29
Combined	Low 2080 × 75% Removal	110	75	148	42
	Low 2080 × 100% Removal	88	80	148	42
	High 2080 × 75% Removal	41	91	83	68
	High 2080 × 100% Removal	35	92	73	71

numbers if protected from climate change are mainly found in the upper subbasin (Fig. 7).

3.4. Current diversity versus future productivity

Under the most extreme scenario, High 2080 × 100% Removal, 8 reaches with viable trajectories under current conditions lost all productivity. These 8 reaches had significantly lower current diversity (0.81 ± 0.31, mean ± SE) than the remaining reaches that maintained productivity under this scenario (2.61 ± 0.43; t = 3.40, p = 0.002).

4. DISCUSSION

4.1. Climate change

Our previous work on the effect of climate change on aquatic habitats in the Umatilla Subbasin indicated that strong effects are expected in the basin's upper areas (DeBano et al. 2016a). These headwater areas are relatively productive under current habitat conditions, producing the greatest number of successful trajectories. Accordingly, climate-induced changes in habitat conditions in these reaches translated to pronounced effects on steelhead performance, demonstrated by declines in basin-wide abundance and capacity across all scenarios. Declines in abundance and capacity were more severe in 2080 than 2040 scenarios. The most extreme climate change scenario (High 2080) reduced equilibrium abundance by approximately 37% relative to current abundance. Other modeling efforts evaluating the effects of climate change on Chinook salmon populations inhabiting similarly sized subbasins in the PNW found similar losses in abundance in northwestern Washington (~40%; Battin et al. 2007) and central Idaho (up to 50%; Crozier et al. 2008). While the EDT model does not estimate extinction probabilities, the current popula-

Table 4. The impact of future scenarios on specific steelhead life stages. Values represent the percent decline in survival of a life stage relative to current conditions. The life stage with the greatest impact from a given scenario is given in **bold**

Scenario	Spawning	Egg incubation	Fry colonization	Parr <1 yr active/summer	Parr ≤1 yr inactive/winter	Parr 1–2 yr active	Parr ≥2 yr active
Low 2040	−3.1	**−12.2**	−1.1	−2.0		−1.2	
Mod 2040	−3.4	**−15.7**	−1.3	−2.7		−1.6	
High 2040	−3.9	**−15.3**	−1.5	−3.3		−2.0	
Low 2080	−4.8	**−18.0**	−2.0	−4.5		−2.5	
Mod 2080	−5.9	**−22.4**	−2.2	−4.9		−2.8	
High 2080	−6.4	**−22.1**	−2.2	−4.7		−2.7	
75% Removal		−4.6	−2.2	−1.0	**−4.8**	−1.6	
100% Removal	−1.5	**−10.8**	−5.6	−3.0	−9.0	−4.4	−2.1
Low 2080 × 75% Removal	−5.3	**−22.9**	−4.1	−5.3	−4.8	−4.0	−1.2
Low 2080 × 100% Removal	−6.2	**−28.4**	−7.3	−7.1	−9.0	−6.7	−2.5
High 2080 × 75% Removal	−6.9	**−27.6**	−4.4	−5.6	−4.8	−4.2	−1.3
High 2080 × 100% Removal	−7.9	**−33.7**	−7.6	−7.4	−9.0	−6.8	−2.6

Table 5. The percentage of 44 reaches in which future scenarios affected the listed survival factors in a way that resulted in moderate (>6% and <25% decrease) and high impacts (≥25% decrease) on steelhead performance. Values are given as moderate impact, high impact

Scenario	Channel stability	Flow	Habitat diversity	Oxygen	Sediment	Temperature
Low 2040	–	–	—	–	13, 18	
Mod 2040	–	–	—	–	18, 22	
High 2040	–	–	—	–	18, 24	
Low 2080	–	–	—	–	27, 34	
Mod 2080	–	–	—	–	20, 47	
High 2080	–	–	—	–	18, 47	
75% Removal	0, 2	–	4, 0	–	7, 2	–
100% Removal	16, 2	2, 0	20, 2	–	13, 7	–
Low 2080 × 75% Removal	0, 2	–	4, 0	–	7, 2	27, 36
Low 2080 × 100% Removal	16, 2	2, 0	18, 2	–	18, 7	25, 36
High 2080 × 75% Removal	0, 2	–	4, 0	–	9, 2	18, 44
High 2080 × 100% Removal	16, 2	2, 0	20, 2	–	16, 7	18, 47

tion of steelhead in the Umatilla Subbasin is not large, and losses of this magnitude may result in an increased probability of extinction. For example, Crozier et al. (2008) found declines in abundance of 20 to 50% were associated with up to 3-fold increases in local extinction probabilities of Chinook salmon populations in Snake River subbasins of Idaho.

Our analysis found that a combination of reduced productivity for successful spawners and a narrowing of trajectory diversity were the drivers of decreased basin-wide abundance under modeled future conditions. Median productivity of successful trajectories was reduced by >50% in 2080 under the most severe climate scenario as compared to current conditions. Trajectory diversity showed similar trends, with median diversity of successful trajectories reduced by ≥35% by 2040, and ≥50% by 2080. These findings are consistent with other studies that predicted that climate change will narrow the range of viable life history pathways available to salmonids in other systems. For example, climate change is predicted to decrease the amount of time conditions are suitable for migration of returning Fraser River sockeye adults (Reed et

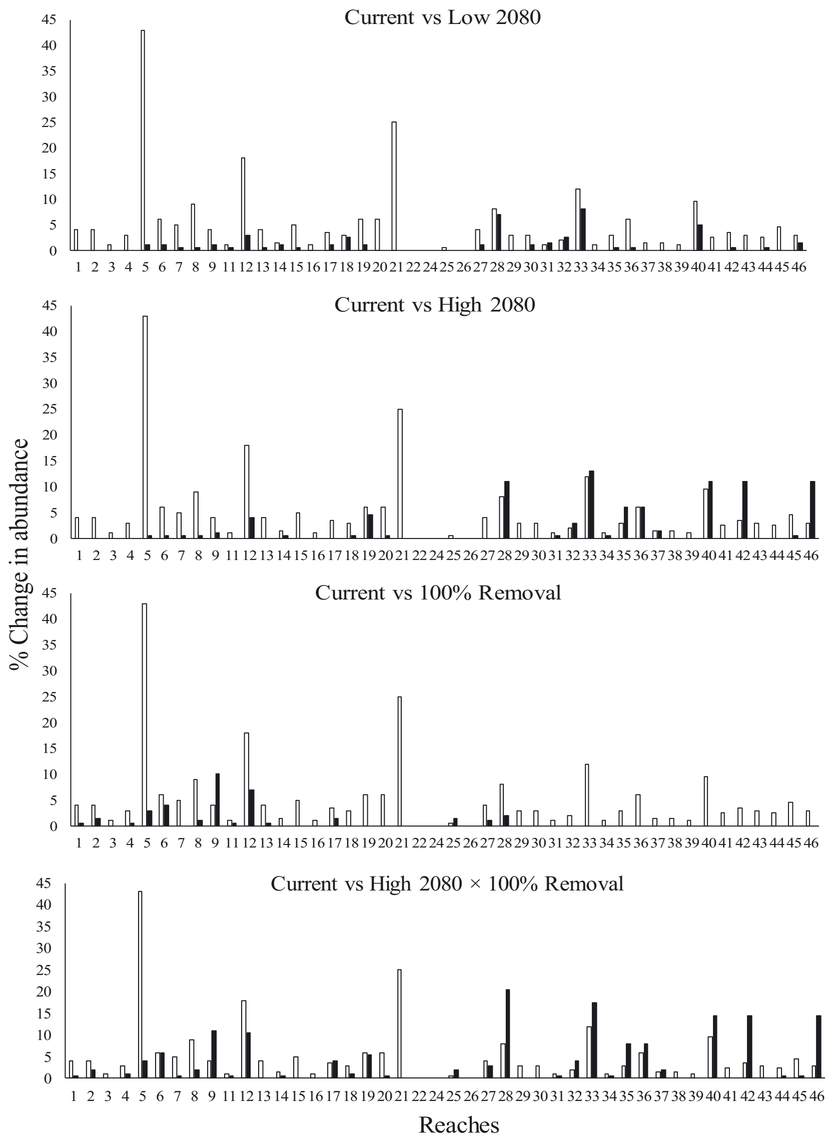

Fig. 7. Reach level restoration and protection priorities identified using the splice analysis for current conditions (clear bars) and 4 future scenarios (filled bars; Low 2080, High 2080, 100% Removal, and High 2080 × 100% Removal). Restoration priorities are based upon the % increase in steelhead abundance if a reach were either restored to historical conditions (for current conditions) or protected in the future to be maintained at current conditions (for the climate change and agricultural intensification scenarios). Reaches are shown on the *x*-axes and are arranged from low elevation to high elevation

al. 2011) and out-migrating Chinook salmon smolts in the Snake River (Achord et al. 2007). In addition, increased water temperatures resulting from climate change can lower life history diversity of steelhead and their freshwater counterparts, rainbow trout (Benjamin et al. 2013).

How climate change affects life-history diversity of salmonids is dependent, at least in part, on the life stages most affected. Spawning adults and incubating eggs were the life stages most vulnerable to our climate change scenarios. These stages are particularly sensitive to warm water temperatures (Richter & Kolmes 2005). Battin et al. (2007) and Honea et al. (2016) examined climate change effects on multiple life stages of Chinook salmon in Washington. As with our study, both studies found that spawners were sensitive to increased water temperatures resulting from climate change. It is possible that our modeling (and that of others) overestimates the impact that increased water temperatures have on salmonid performance. In the present study steelhead performance responded to modeled maximum summer water temperatures which were applied across entire reaches. However, in many river systems, water temperatures are not homogeneous across reaches, but contain areas of warm water and pockets of relatively cool water resulting from groundwater seeps, hyporheic flows, cold-water tributaries, and other factors (Bilby 1984). These cool-water pockets can provide important thermal refugia for salmonids, allowing them to inhabit areas that at a larger scale appear too warm (Torgersen et al. 1999, Sutton et al. 2007). These fine-scale thermal refuges are potentially important enough to the survival of salmonids and other cold-water fish that their management and enhancement is a topic of current research (Kurylyk et al. 2015). It was beyond the scope of the current study to attempt to model water temperatures at a fine enough scale to identify and incorporate cold-water pockets in the Umatilla River reaches. However, this is an important area of study, and modeling for future work on the impacts of climate change on cold-water fish species.

As in our study, Battin et al. (2007) found that incubating eggs were sensitive to climate change impacts. However, in contrast to our findings, Battin et al. (2007) found that the impact of climate change on egg mortality was most likely the result of increases in peak flows that would scour eggs from redds and not, necessarily, from increases in water temperature. It is uncertain whether steelhead egg incubation in the Umatilla River would be similarly affected by peak flows (because our model did not include climate change induced high flow events). However, it is likely that earlier and greater magnitude scouring flows in late winter would have additional negative effects on steelhead in the Umatilla Subbasin, since spawning can occur as early as mid-February (DeBano & Wooster 2004).

The spatially explicit nature of EDT modeling allowed an examination of specific reaches in the Umatilla Subbasin. A number of reaches in the mid- and upper basin were high quality as defined by high productivities (≥5.0) of successful trajectories. Climate change decreased the extent of highly productive habitat by 12 to 91%. In addition, under current conditions, these highly productive reaches are distributed across several large contiguous areas. However, under climate change scenarios, the most productive habitats retreated to isolated and fragmented refugia in high-elevation, low-order tributaries. Modeling of other systems has predicted similar loss and fragmentation of high quality habitat at watershed scales under climate change (Wenger et al. 2011a, Ruesch et al. 2012, Lawrence et al. 2014). These predicted biological effects are consistent with observed changes in the distribution of thermally sensitive species in the Rocky Mountains of the USA and in France in response to changing climate (Eby et al. 2014, Grenouillet & Comte 2014, respectively).

Some strongholds of productivity were maintained in smaller, high elevation reaches under climate change. These reaches might be most resistant to climate change because they are well-shaded and fed by groundwater coming from springs and seeps (Luce et al. 2014, Isaak et al. 2016). Indeed, Isaak et al. (2015) consider these high-elevation areas as important cold-water refugia for salmonids in the Rocky Mountains. However, not all reaches with high productivity in current conditions maintained high productivity under climate change. Because of variation in solar radiation input and flow, some reaches experienced higher water temperatures and greater declines in steelhead performance compared to nearby reaches that exhibited smaller changes in water temperature and remained high quality habitat. This illustrates one of the key advantages of EDT modeling; it not only quantifies habitat loss under different climate change scenarios, but also identifies specific areas that serve as strongholds of steelhead productivity in the future, as well as those most vulnerable to climate change.

4.2. Agricultural intensification

Agricultural intensification also had pronounced effects on steelhead in the Umatilla Subbasin, lowering basin-wide abundance and median reach productivity and trajectory diversity. While agricultural intensification was modeled to occur in the lower and mid-basin, and steelhead mainly use the upper basin for spawning and rearing, there were several mid-elevation reaches important to steelhead productivity in the basin that were directly impacted by agricultural intensification. Under the 100% Removal scenario, these reaches lost large amounts of productivity and diversity. In addition, steelhead productivity and diversity in several reaches outside of the agricultural intensification area were impacted by agricultural intensification. These performance decreases can be driven by juveniles' use of reaches in the lower subbasin that have been directly impacted by agriculture, as well as negative effects experienced by individuals moving through impacted reaches (e.g. spawning adults, outmigrating juveniles).

The main drivers of decreased steelhead performance with agricultural intensification were changes in sediment load, channel stability, and habitat diversity. Riparian vegetation effectively buffers stream reaches from sediment input, provides habitat for fish through exposed root systems and inputs of large woody debris, and stabilizes stream banks reducing the likelihood of bank failure (Gregory et al. 1991, Pusey & Arthington 2003). The life stages most vulnerable to agricultural intensification were incubating eggs and overwintering parr in their first year. Sediment deposition on incubating eggs lowers the levels of dissolved oxygen surrounding the eggs, reducing their survival (Peterson & Quinn 1996, Jensen et al. 2009). In addition, suspended sediment has a number of physiological effects on salmonid juveniles including reduction in feeding and growth rates and damage to gills (Newcombe & MacDonald 1991). Large woody debris and exposed rootwads provide important cover for juvenile salmonids from predation and high winter flows, and the presence of this shelter enhances the abundance of juvenile salmonids (Roni et al. 2015, Gonzalez et al. 2017).

We modeled agricultural intensification only as a decline in the amount of riparian vegetation present in the lower basin. However, it is likely that agricultural intensification will also have other effects on the Umatilla River that are expected to negatively impact steelhead and other salmonids. These other effects include changes in the amount and type of agrochemicals applied to fields and changes to instream flows resulting from increased irrigation. Given the uncertainty of the magnitude of these effects and their relationship to river reach habitat, we chose not to include them in our current modeling effort. However, we note that more work is needed to quantify additional agricultural effects, and their interactions with each other, on river ecosystems.

4.3. Interactions: climate change and agricultural intensification

Combined, climate change and agricultural intensification had stronger impacts on steelhead performance in the Umatilla Subbasin than either stressor had independently. For example, basin-wide abundance of steelhead was reduced from current conditions by 37% under the most severe climate change scenario in 2080, and by 27% under the 100% Removal scenario. When these 2 scenarios were combined, steelhead abundance was reduced by 57%. The synergistic nature of these 2 stressors coincides with our earlier work on the spatial complementarity of these 2 stressors on the river environment (DeBano et al. 2016a). However, it was not clear *a priori* whether these 2 stressors would have synergistic effects on steelhead, given that agricultural intensification was modeled for the lower and mid-basin only, areas in which many reaches are currently poor habitat for steelhead. The synergistic nature of the 2 stressors and the possibility of agricultural intensification in the future in the Umatilla Subbasin indicates that this subbasin (and many subbasins in the Columbia River Basin) will be a particularly challenging habitat for steelhead in the future.

Other work on interaction effects of climate change and local stressors on freshwater biota is limited, despite the likelihood that local factors will change in many areas in concert with climate change. Walters et al. (2013) modeled the combined impacts of climate change and water diversion on Chinook salmon in the Lemhi River in Idaho, USA and found synergistic effects on both juvenile survival and habitat carrying capacity. Likewise, Mantyka-Pringle et al. (2014) found synergistic effects of climate change and increased urbanization/riparian buffer removal on fish diversity in Australia. Nelson et al. (2009) also found interactive effects of increased urbanization and climate change that are predicted to affect a majority of the stream fish species in the Chesapeake Bay region. However, response to the 2 stressors combined in that study were variable and depended upon the specific climate change scenario modeled (Nelson et al. 2009). The impact of climate change and invasive fish species on native salmonids in the PNW has also received attention (Wenger et al.

2011b, Lawrence et al. 2014). However, because these studies did not examine each stressor individually, it is not clear whether interactions between these stressors are synergistic. Regardless, the authors of both studies conclude that non-native fish are important in driving declining distributions of native salmonids, and that this trend will continue in the future under climate change.

4.4. Trajectory diversity and productivity

Reaches that maintained productivity under the most severe future scenario — High 2080 × 100% Removal — had significantly higher current life history diversity than reaches that lost all productivity under this scenario. This indicates that reaches that allow steelhead to 'spread risk' across a variety of life-history pathways are resistant to environmental changes, as suggested by conceptual and theoretical work (den Boer 1968, Fox 2005). This finding suggests that examining life history diversity is essential in determining which areas are most important for protection and restoration. While average productivity is also important, reaches with high average productivity can have relatively low diversities, leading to a high risk of losing all productivity under environmental change.

Our results indicate that the relationship between diversity and future productivity holds at a relatively small scale. Work with sockeye salmon in Bristol Bay, Alaska indicates that this relationship is also found at increasingly larger scales. Greene et al. (2010) found that sockeye populations in the Bristol Bay region with more life-history diversity had the greatest productivity and least variability in productivity through time. At a larger scale, Hilborn et al. (2003) suggest that the Bristol Bay sockeye fishery has been sustainable for decades because of the large variety of life history strategies displayed by the hundreds of different sockeye populations that comprise this fishery.

5. MANAGEMENT IMPLICATIONS

5.1. Preservation and restoration under changing climate and expanding agriculture

A strength of the EDT approach is that it identifies areas in the basin most important to steelhead performance in future scenarios by 'splicing' current conditions into each reach individually and evaluating steelhead performance. Reaches that enhance steelhead performance are those that are important to protect in their current state or to restore to their current state under different scenarios. Our results identified a number of reaches in the upper basin as important for protection of steelhead performance in the context of climate change. In contrast, areas important for protection under agricultural intensification were largely limited to the lower and mid-basin. Understanding how and where future stressors will likely affect species of interest is necessary for managing these species and deciding how limited conservation funds should be used. In the original use of EDT for the Umatilla Subbasin (during the NWPCC subbasin planning effort for the Columbia Basin; DeBano & Wooster 2004, NWPCC 2005) reaches were identified for restoration based upon 'splicing' historic conditions for each reach individually into current conditions (DeBano & Wooster 2004). Our results indicate that reaches important to protect from future climate change are not necessarily the same areas as those currently identified as important to restore to historic conditions. While this might be viewed as a conundrum to land managers with limited funding to restore and protect river reaches, it simply highlights the need to consider both future conditions as well as current conditions when developing river management plans. Beechie et al. (2013) addressed this issue by developing a decision support framework designed to determine whether management and restoration plans addressing current environmental stressors will also ameliorate predicted conditions resulting from climate change. In general, the authors found that restoration actions designed to restore floodplain connectivity and more natural streamflow regimes, and to re-aggrade incised channels were most likely to ameliorate the influences of climate change on stream temperatures and flow.

These restoration actions designed to address climate effects on stream temperature would likely work in the Umatilla Subbasin. Many reaches of the Umatilla River and its tributaries lack floodplain connectivity and are incised (DeBano & Wooster 2004). Indeed, recent restoration efforts in one of the Umatilla River's primary tributaries was designed to promote increased floodplain-channel connectivity to, in part, lower stream temperatures (Confederated Tribes of the Umatilla Indian Reservation 2014).

5.2. Management and multiple stressors

Many ecosystems are being adversely affected by climate change and those effects will likely increase in the future (Scholze et al. 2006). In many areas, local stressors will also increase in the future to support a burgeoning human population. Given this, it is imperative to develop a better understanding of how climate change and local stressors interact to influence species of interest and other natural resources. We found that climate change and agricultural intensification had synergistic effects on steelhead performance resulting from a spatial complementarity of the 2 stressors (results reported here and in DeBano et al. 2016a). Walters et al. (2013) also found synergistic effects of climate change and water diversion for irrigation on Chinook salmon in an Idaho river system. However, local stressors and climate change will not necessarily be synergistic in all systems. In some cases, effects of climate change might overwhelm the effects of local stressors (e.g. some scenarios in Nelson et al. 2009).

Generalizing responses of systems to combined effects of climate change and local stressors will be challenging, with responses likely influenced by which climate change effects are manifested, the type of local stressor, and the system/species-specific characteristics being examined. Models, such as EDT, allow regional users to explore multiple scenarios, including highly variable predictions about precipitation and temperature changes associated with climate change, to assess a broad range of possibilities that take into account the peculiarities of their system. Future modeling efforts should be combined with empirical work focusing on changes in salmonid distributions, abundances, and the timing of life cycles to provide a better understanding of how multiple stressors may interact in an uncertain future.

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