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Simulating riparian vegetation and aquatic habitat dynamics in response to natural and anthropogenic disturbance regimes in the Upper Grande Ronde River, Oregon, USA

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Abstract

We developed state and transition models (STMs) to evaluate the effects of natural disturbances and land-use practices on aquatic and riparian habitats. The STMs consisted of discrete states defined by channel morphology and riparian vegetation. Transitions between states resulted from plant succession and from natural and anthropogenic disturbances. Channel conditions and habitat suitability for anadromous salmonids were ranked by using a qualitative four-factor scale for each state in the STMs. Disturbance probabilities were varied to define both historical and current disturbance regimes. Models were run for 120 years with the current disturbance regime to illustrate changes associated with Euro-American settlement, and then run for an additional 50 years under the historical disturbance regime to illustrate the potential for passive recovery. Results suggested that Euro-American settlement dramatically changed riparian vegetation and channel conditions, which resulted in substantial declines in habitat quality. Passive recovery of channel conditions and habitat suitability was quick in some stream types, but slow in others. Overall, our results underestimate the effects of human land uses on streams and overestimate the rate of recovery under passive restoration because the models do not yet include the effects of many management activities, especially those resulting from forest harvest and roads.
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1. Introduction

Populations of Pacific salmonids have declined in abundance or were eliminated from much of their historical range, and many populations within the interior Columbia River basin are now listed under the U.S. Endangered Species Act (USDA and USDI, 2000). Populations of other native fishes have also declined (Lee et al., 1997). Many factors have contributed to these declines, including the degradation of spawning and rearing habitat in tributary streams (Federal Caucus, 2000). Thus, the maintenance of existing high-quality habitat and restoration of degraded habitat in the upper tributaries of river networks is an important component of salmonid conservation efforts. Land management decisions in the interior Columbia River basin occur in ecosystems that have high natural variability and also have been altered by historical and current land and water management prac-

tices. Consequently, predicting potential management effects on tributary habitat is fraught with uncertainty about the ecologic responses and the complexity of multiple management objectives and strategies under consideration (Rieman et al., 2001; Wissmar and Bisson, 2003). To aid evaluations, land managers might use tools that formalize complex relationships in a common framework that describes aquatic habitat in the context of landscape processes and conditions, potential effects of management actions, and sources of uncertainty.

Few analytical tools are available to assess conditions of aquatic habitats for anadromous salmonids at mid to fine scales (i.e., 4th–6th-field hydrologic units ranging in size from 5000 to 500,000 ha). Existing tools allow assessment of current conditions and monitoring (e.g., Kershner et al., 2004; Reeves et al., 2004) or projecting impacts from specific disturbances or activities (e.g., Lancaster et al., 2001; Spies et al., 2002). Existing models, however, do not project the future effects of natural disturbances and land-use practices typical of the interior Columbia River basin. An alternative approach that has been applied in vegetation analyses of forest and rangeland ecosystems in the

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interior Columbia River basin uses state and transition models (STMs) (Hann et al., 1997; Hemstrom et al., 2001). In these analyses, STMs are developed for each potential vegetation group (e.g., a forest or rangeland type). Each STM is composed of a number of distinct states defined by vegetation structure and composition. States are connected by transition probabilities that reflect plant succession and both natural and anthropogenic disturbances. To date, these modeling efforts have not included riparian zones.

The objective of this study was to explore the use of STMs to evaluate the effects of natural disturbances and land-use practices on aquatic and riparian habitats. Stream reaches can be placed into similar groups by using existing classifications of riparian vegetation (Crowe and Clausnitzer, 1997) and geomorphic classifications for mountain streams (Montgomery and Buffington, 1997, 1998). The range of channel and vegetation types that can occur within a group can be broken into discreet states based on channel-morphologic features and on the structure and composition of the riparian vegetation. Finally, transitions between states can be defined by the rates of the underlying geomorphic processes and interactions between the geomorphic processes, riparian vegetation, and a variety of disturbances. This approach is attractive because the models are relatively simple to develop and run, making them easily portable to a variety of landscape analyses. Further, the aquatic–riparian STMs could be linked directly into existing landscape–scale modeling efforts by using upland STMs (Hemstrom et al., 2006).

Substantial questions surround the utility of the STM approach for characterizing the dynamics of streams and their riparian zones in response to natural disturbances and land-use practices. The STM models are "deterministic" in that disturbances and succession force transitions between pre-specified states. The use of STMs to explore plant community dynamics is well supported by both theory and empirical research that documents equilibrium and non-equilibrium responses of plant communities to succession and disturbance. Similarly, a general understanding of dynamic responses to disturbance, and the dynamic equilibrium between channel morphology and the balance between sediment supply and transport capacity are well developed in geomorphology. Geomorphologists, however, have not traditionally viewed stream networks as collections of patches that have distinct states linked by transitions forced by disturbances and recovery from those disturbances. Consequently, the aquatic–riparian STMs presented here should be considered formalized hypotheses of the states possible for any given stream reach and the variety of processes that influence those states.

2. Methods

2.1. Model development

2.1.1. Development of potential channel-morphologic groups

Identification of potential channel-morphologic groups was based on a widely used stream classification scheme that links reach types to the geomorphic processes that formed them (Montgomery and Buffington, 1997, 1998). We build on the foundation of this hierarchical, process-based reach classification to develop potential channel-morphologic groups.

Channel-reach morphology broadly results from the balance between sediment supply and transport capacity (Montgomery and Buffington, 1998). Within a physiographic province, where bedrock lithology, climate, topographic relief, and the relation between watershed area and discharge are relatively uniform, both sediment supply and transport capacity will show sufficiently characteristic patterns so that reach slope, channel constraint (the width of the channel relative to the width of the floodplain), and watershed area will be the primary determinants of channel morphology (Chartrand and Whiting, 2000; Montgomery and Buffington, 1998). We followed Montgomery et al. (1999), and used reach-averaged stream gradient to define the following potential channel-morphologic groups: cascade, step-pool, plane-bed, and pool-riffle. We further refined the break between plane-bed and pool-riffle groups on the basis of watershed area following Montgomery and Buffington (1997) who reported that plane-bed channels seldom occurred at watershed areas greater than 3000–4000 ha.

We recognize that channel response is highly variable and that reach morphology is not solely a function of watershed area, channel slope, and constraint. This may lead to substantial overlap among channel-morphologic groups. Data presented in Montgomery and Buffington (1997, 1998) and by Chartrand and Whiting (2000) were collected in areas with different climate and geology so that stream morphologies within the Upper Grande Ronde River are unlikely to match exactly the relation with slope and watershed area observed in either of these studies. However, the reach types described by Montgomery and Buffington (1997) are based on geomorphic processes and are generally applicable to mountain stream networks. We stress that a high degree of classification certainty is not necessary to meet our primary objective of developing prototype aquatic–riparian STMs. The application of these prototype models to the Upper Grande Ronde River is intended only as an example to illustrate their potential application in assessing habitat conditions in a real-stream network.

2.1.1.1. Cascades. Cascade channels are characterized by rough beds with disorganized structure composed of boulders or large cobbles that result in highly turbulent flow. They are very resistant to change (Buffington et al., 2002) owing to the size of streambed sediment (Montgomery and Buffington, 1998), steep gradients that limit sediment deposition (Montgomery et al., 1996), narrow valley floors that provide little space for sediment deposition, and because deposited sediment is quickly scoured from the channel because of the high transport capacity (Buffington et al., 2002). Cascade channels are important sources of sediment and large wood for channels lower in the stream network (Reeves et al., 2003). Cascade reaches span a wide range of channel gradients, from less than 6.5% to more than 20%, and were subdivided to distinguish lower and higher gradient cascades. High-gradient cascades were those channels with longitudinal gradients in excess of 12%, and comprised

9% of the perennial stream network. Channels with gradients between 6.5 and 12%, in watersheds up to 12,800 ha, can be in a forced step-pool state if large wood is present in the channel. In this case, the channels are responsive to changes in sediment supply and discharge because large logs control sediment storage (Montgomery et al., 1996) and the occurrence of pools. Low-gradient cascade channels comprise 27% of the perennial stream network.

2.1.1.2. Step-pools. Step-pool reaches are highly organized, with a free-formed step-pool structure. The bed is usually armored with gravels and cobbles that are only mobilized during infrequent, large floods so that in most years, finer bedload sediment is transported over the armored surface (Montgomery et al., 1999). Logs and log jams frequently obstruct these channels, forming steps in the longitudinal profile. Sediment accumulates above the obstruction, and plunge pools are scoured into the bed sediment below the steps. Reaches with abundant large wood may have more frequent pools than reaches with little wood (Buffington et al., 2002). We classified reaches with gradient between 3.0 and 6.5% as step-pool reaches, and these channels constitute 34% of the perennial stream network.

2.1.1.3. Plane-beds. Plane-bed reaches are transitional between sediment source and response process domains (Montgomery, 1999). These reaches lack notable bedforms so that channel units are described as glides, runs, riffles, or rapids (Hawkins et al., 1993). Pools are infrequent. These reaches are highly sensitive to wood loading (Buffington et al., 2002; Montgomery et al., 1995), which forces the development of a pool-riffle state. We classified reaches with drainage areas less than 3200 ha and average gradients between 1.5 and 3% as plane-bed reaches. These channels comprise 12% of the perennial stream network.

2.1.1.4. Pool-riffles. Pool-riffle reaches have sinuous channels with point bars inside of meander bends that create an alternating series of free-formed riffles and pools. These reaches are highly responsive to changes in sediment supply and discharge (Montgomery, 1999). Large logs or log jams contribute to pool formation so that reaches with abundant large wood typically have more frequent pools and greater pool volume than reaches with little wood (Buffington et al., 2002). We classified reaches with gradients less than 1.5%, and reaches with gradients between 1.5 and 3% with drainage areas greater than 3200 ha as pool-riffle reaches. These reaches account for 15% of the perennial stream network.

2.1.1.5. Wet meadows. We considered reaches with longitudinal gradients less than 0.6% as a special case of the pool-riffle potential morphologic group that we called wet meadow reaches. In an unincised condition, we assumed that water tables were near the soil surface year round and that saturated soils would prevent establishment of conifers, maintaining broad, lowland meadows with highly sinuous channels. Without a local source of recruitment, large wood was uncommon. Rather, pools developed in channel meanders where undercut banks, roots, and overhanging vegetation provided pool structure. In some cases, especially following major floods, channels cut down into the floodplain, leading to lowered water tables, drying of upper soil horizons, and conifer invasion. These reaches constitute only 2% of the perennial stream network.

2.1.2. Riparian potential vegetation groups

The potential channel-morphologic groups described above can occur over a wide range of elevations so that the potential number of riparian and adjacent upland vegetation types adjacent to the stream is enormous. Constructing a model for every combination of potential channel-morphologic group and potential vegetation group was prohibitively difficult. To simplify the task, we built a generic riparian forest potential vegetation group, a wet meadow potential vegetation group, and a dry meadow potential vegetation group.

Our forest potential vegetation group is based on the cool-moist forest described by Hemstrom et al. (2006). Grand fir (*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) dominate late-successional conditions in cool-moist forests. Western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*) are common early successional species and can remain important components of stands over hundreds of years, especially on drier sites. Several hardwood species are common in riparian areas, especially willows (*Salix* spp.) and alders (*Alnus* spp.) (Crowe and Clausnitzer, 1997; Kovalchik and Clausnitzer, 2004). We grouped conifers as either shade intolerant (larch, lodgepole, and ponderosa pine) or relatively shade tolerant (grand fir and Douglas-fir). All riparian hardwoods, including both shrubs and small trees, were combined into a single functional group.

A variety of meadow vegetation communities are common within mountain stream valleys of the Blue Mountains (Crowe and Clausnitzer, 1997), but we combined these into two meadow potential vegetation groups that consist of a variety of meadow and shrub-meadow states. Within the wet meadow potential vegetation group, the wet meadow states are dominated by sedges (*Carex* spp.) and willows. In the dry meadow potential vegetation group, the dry meadow states are dominated by a variety of native perennial bunch grasses (e.g., *Festuca* spp., *Bromus* spp., and others) with willow and alder along streambanks.

2.1.3. Aquatic–riparian state and transition models

State and transition models were developed for each potential channel-morphologic group. Separate STMs were developed for high-gradient and low-gradient cascades because the wood-forced step-pool states occurred only in the low-gradient cascades (Table 1). We also developed separate STMs for constrained and unconstrained channels (see Section 2.2.1. for details) for both the step-pool and cascade with wood-forced step-pool models (Table 1). We followed the convention of Hemstrom et al. (2006) and developed models by using the Vegetation Development Dynamics Tool (VDDT) (Beukema et al., 2003), a non-spatial modeling framework that allows building and testing of STMs. Succession is treated as a deterministic process in VDDT, where, in the absence of disturbance, only time is required to develop from one state to the next. Without distur-

Table 1
Relationships between the five potential morphologic groupings of channel types and the state and transition models used to describe those channels; the number of meadow, pioneer-forb, and forest states; and the lengths of the perennial stream network and fish-bearing stream network

Potential morphologic group	State and transition model	Meadow states	Pioneer-forb states	Forest states	Total	Total network length (%)	Fish-bearing length (%)
Wet meadow	Wet meadow	5	5	20	30	2	5
Pool-riffle	Pool-riffle	10	6	30	46	15	36
Plane-bed	Plane-bed	10	6	30	46	12	19
Step-pool	Unconstrained		4	20	24	12	29
	Constrained		4	16	20	22	0
Cascade	Unconstrained with wood-forced step-pool		4	20	24	1	3
	Constrained with wood-forced step-pool		4	16	20	26	7
	Cascade		4	16	20	9	0

bance, all vegetation eventually accumulates in a single stable state. Disturbances are modeled as stochastic events with specified occurrence probabilities that force state transitions along predetermined pathways. Our states include geomorphic conditions of the channel and valley floor, and our disturbances include a suite of hydro-geomorphic events that trigger changes in both riparian vegetation and channel and valley floor morphology.

2.1.3.1. Successional trajectories. Successional patterns of the generic riparian forest broadly follow those of the cool-moist coniferous forest potential vegetation group described by Hemstrom et al. (2006). In general, pioneer-forb communities (a mix of native and exotic forbs and grasses) initially dominate following stand-replacing disturbances (Tables 2–4). Stand-initiation commences with regeneration of shade-intolerant conifers. We track the presence of snags in both the pioneer-forb and stand-initiation structural classes, recognizing distinct states with and without snags. After 46 years of tree growth, stands

reach a stem-exclusion structural state where the closed, dense canopy excludes further establishment of conifers (Table 2). In this state, large snags from the previous forest have mostly disappeared, and although mortality of newly established trees may be substantial, these trees are too small to provide wood large enough to shape channel morphology.

With increasing time, density-dependent mortality thins the stand and opens the canopy, rejuvenating understory growth and initiating establishment and growth of shade-tolerant conifers (Table 2). At successional ages between 119 and 175 years, the stand is in a young-multistrata structural state composed of both shade-tolerant and shade-intolerant conifers. In this state, trees are large enough so that wood recruited to the stream is geomorphologically functional. Starting at 176 years, the stand progresses to an old-multistrata structural state dominated by large conifers where the structural elements of the stand confer old-growth characteristics that will persist indefinitely in the absence of stand-replacing disturbances (Table 2).

Table 2
Primary transition probabilities used in each structural state of the state and transition models (STMs) describing succession and disturbance-induced changes of the generic riparian forest

	Vegetative structural state											
	Pioneer-forb		Stand initiation with snags		Stand initiation without snags		Stem-exclusion		Young-multistrata forest		Old-multistrata forest	
	H	C	H	C	H	C	H	C	H	C	H	C
Successional age range (years)	0		1–20		1–46		47–118		119–175		176–500	
Hardwood and conifer recruitment	0.0688	0.0688										
Riparian hardwood recruitment			0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Large wood recruitment	0.1	0.1	0.1	0.1					0.02	0.02	0.05	0.05
Successional-change grazing				0.2		0.2		0.045		0.045		0.045
Wildfire—underburn	0.014	0.007	0.014	0.007	0.014	0.007	0.016	0.008	0.014	0.007	0.0111	0.0056
Wildfire—stand-replacing			0.006	0.003	0.006	0.003	0.0066	0.0033	0.0089	0.0044	0.0111	0.0056
Major flood	0.02	0.02	0.015	0.015	0.015	0.015	0.01	0.01	0.01	0.01	0.01	0.01
Debris flow–with large wood	0.003	0.0015	0.003	0.0015	0.003	0.0015	0.003	0.0015	0.003	0.0015	0.003	0.0015
Debris flow—no wood		0.0015		0.0015		0.0015		0.0015		0.0015		0.0015
Depositional flood (wet meadow PMG only)												
Channels with large wood									0.001	0.001	0.001	0.001
Channels without large wood							0.004	0.004	0.004	0.004	0.004	0.004

Forest ages of each structural state are given, as are transition probabilities ($0 \leq p \leq 1$) under current (C) land management practices and under historical (H) conditions. Values represent the annual probability that a given event will lead to a state change within the STM and do not represent the probability of occurrence for a given disturbance (PMG: potential channel-morphologic group).

Table 3

Primary transition probabilities used in each structural state of the state and transition models describing succession and disturbance-induced changes in non-forest vegetation states of the wet meadow potential channel-morphologic group

| | Vegetative structural state | | | | | | | |
| | Pioneer-forb | | Kentucky bluegrass | | Sedge remnant willow | | Willow-sedge wet meadow | |
	H	C	H	C	H	C	H	C
Successional age range (years)	0–4		5–19		5–19		20+	
Hardwood and conifer recruitment	Conifers none/willow recruitment as part of successional recovery							
Erosional flood with channel incision	0.01	0.01	0.004	0.004	0.004	0.004	0.004	0.004
Successional-change grazing		0.2		0.2		0.2		0.05

Format and abbreviations follow Table 1.

Riparian zones of three of the potential channel-morphologic groups (wet meadow, pool-riffle, and plane-bed) include meadow or shrub-meadow vegetation states. The wet meadow states have high water tables and frequent saturation to the soil surface leading to dominance by sedges. Soil saturation prevents conifer establishment in the wet meadow states and willows are the dominant shrub, except in soils that are saturated year round. With high water tables, succession is rapid in absence of disturbances, requiring only 20 years to re-establish willow-sedge communities from the pioneer-forb community (Table 3). Channel incision lowers the water table, converting wet meadow states into dry meadow states and opens the riparian area to conifer establishment.

Only dry meadow states occur in the pool-riffle and plane-bed potential morphologic groups. These are dominated by native perennial bunch grasses, alders, and willows. The successional trajectory from pioneer-forb communities to the willow-native bunch grass meadows takes 80 years, much longer than in the wet meadows, because low soil moisture more strongly limits plant growth over the growing season (Table 4). We assumed that shade-intolerant conifers could establish in all dry meadow states. Once conifers are established in dry meadow states, successional trajectories follow those described above for the generic riparian forest.

2.1.3.2. Disturbance regimes. We included grazing, major floods, debris flows, and wildfire disturbances in our aquatic–riparian STMs (Tables 2–4). Domestic livestock, elk,

and deer can substantially affect understory vegetation in both uplands and riparian zones (Brookshire et al., 2002; Hessburg and Agee, 2003; Riggs et al., 2000). Grazing can also affect channel morphology through changes in riparian vegetation combined with channel-forming floods and physical trampling of streambanks (see reviews and references cited by Belsky et al., 1999; Kauffman and Krueger, 1984; Trimble and Mendel, 1995; Wondzell, 2001). Our models include grazing-related transitions that remove riparian hardwoods and convert sedge or grass dominated meadows to pioneer-forb communities (Tables 2–4). Unfortunately, little is known about historical grazing pressure from native ungulates, although there is some indication that herbivory was relatively low in the interior Columbia River basin prior to Euro-American settlement (Belsky and Blumenthal, 1997; Mack and Thompson, 1982). We assumed that the impact of native herbivores would have been dramatically less than that of domestic livestock, both because fewer animals were present and because with more of the landscape in grasslands and shrublands (Hessburg and Agee, 2003), more forage would have been available so that riparian hardwoods would have been less affected. Therefore, successional-change grazing is not included in the historical disturbance regime (Tables 2–4). We did not directly model recovery from grazing. Instead, recovery occurs from plant succession in the absence of grazing.

Our models include disturbances from both underburns and stand-replacing wildfires, the occurrence of which is dependent on stand structure (and therefore fuel conditions) (Table 2). We assumed that reoccurrence intervals were the same in riparian

Table 4

Primary transition probabilities used in each structural state of the state and transition models describing succession and disturbance-induced changes in non-forest vegetation states of the pool-riffle and plane-bed potential channel-morphologic groups

| | Vegetative structural state | | | | | | | |
| | Pioneer-forb | | Kentucky bluegrass | | Perennial bunch grass remnant willow | | Willow and perennial bunch grass | |
	H	C	H	C	H	C	H	C
Successional age range (years)	0–20		21–49		50–79		80+	
Willow and riparian hardwood recruitment	Willow recruitment as part of successional recovery							
Conifer recruitment	0.0688	0.0688	0.01	0.01	0.01	0.01	0.01	0.01
Successional-change grazing		0.2		0.1		0.1		0.1
Wildfire–underburn	0.014	0.007	0.014	0.007	0.014	0.007	0.014	0.007
Major flood	0.02	0.02	0.015	0.015	0. 01	0. 01		

Format and abbreviations follow Table 1.

areas as in adjacent uplands, as shown by Olson (2000) for dry forest types in the Blue Mountains. Therefore, we used reoccurrence intervals for the cool-moist potential vegetation group from Hemstrom et al. (2006). Under current forest management practices, fire suppression reduces the reoccurrence intervals of wildfires, which we simulate by setting the transition probabilities under current conditions to one-half of those under historical conditions (Table 2). Stand-replacing fires kill most above-ground vegetation and reset the plant community to the pioneer-forb state. Underburns kill all regenerating conifers in dry meadow states (Table 4) but do not affect state transitions in any other riparian states.

Our models include the effects of debris flows, which are important processes shaping stream channels in mountainous landscapes because they can deliver substantial amounts of wood and sediment to stream networks (Reeves et al., 1995, 2003). Estimates of reoccurrence intervals in moist, maritime climates range from less than 100 years to longer than 350 years (May and Gresswell, 2004; Swanson et al., 1982). In drier, continental climates, debris flows usually occur where intense storms affect areas recently burned by stand-replacing wildfires (see review and references cited by Wondzell and King, 2003). Stand-replacing wildfires occur once every 90–300 years in the cool-moist conifer forests. We do not know of any estimates of debris flow reoccurrence intervals for the Blue Mountains or for similar landscapes under continental climate regimes. Therefore, we set the debris flow reoccurrence interval at 333 years (Table 2), a conservative interval longer than that of stand-replacing wildfire and similar to the longer debris flow reoccurrence intervals observed in maritime climates. We included the effect of forest harvest and salvage logging by having half of the debris flows under the current disturbance regime be "wood-free", in that they do not deliver large wood to the receiving channel (Table 2). Debris flows were only simulated in high-gradient channels (step-pools and cascades). In unconstrained channels, debris flows removed riparian hardwoods along the channel but did not affect remaining riparian vegetation. In constrained channels, however, debris flows removed all riparian vegetation from the full width of the floodplain, resetting the vegetation to the pioneer-forb state. Debris flows with wood added large wood to streams where it was previously lacking, whereas debris flows without wood removed large wood from streams either by transporting it downstream or moving it laterally, out of the channel. We did not directly model recovery from debris flows. Instead, we assumed that recovery of channel conditions would parallel vegetative recovery.

Major floods shape stream channels in mountainous areas (Johnson et al., 2000; Wondzell and Swanson, 1999), but their effects can be modified by riparian vegetation which can stabilize streambanks, limit bank erosion, and create depositional zones for fine sediment (Clifton, 1989; Gregory et al., 1991; Platts et al., 1985). Conversely, poorly vegetated streambanks are prone to erosion, leading to channel widening or incision during major floods (Elmore and Beschta, 1987; Platts et al., 1985; Trimble and Mendel, 1995). Finally, major floods, especially if combined with enhanced sediment delivery to channels,

can rework bed and bank sediment, knock down streambank trees, pile large wood into jams on gravel bars and floodplains outside the wetted channel, and form wider and shallower channels. We were unable to find any published estimates of the flood magnitudes (or reoccurrence intervals) required to drive major changes in channel morphology. Major floods were only simulated in wet meadow, pool-riffle, and plane-bed channels. We simulated the control of vegetation on flood effects by decreasing the probability that a state change would result from a major flood with successional development of vegetation (Table 2). We did not directly model recovery from major floods. Instead, we assumed that recovery of channel conditions would parallel vegetative recovery. We simulated major floods in wet meadows differently, because of the sensitivity of water table heights to channel incision and aggradation. We simulated erosional floods that drove channel incision in wet meadow states, the probability of which varied with the successional status of the vegetation (Table 3). Recovery from incision was simulated through depositional floods that drove channel aggradation where channels had been incised through an earlier erosional flood, but where subsequent vegetation growth had stabilized streambanks or allowed recruitment of abundant large wood to channels (Table 2).

We simulated recruitment of large wood as a stochastic process, similar to the other disturbances (Table 2). The morphologic state of forested streams is often controlled by the presence of large logs or log jams that can force the morphology of low-gradient cascade channels toward step-pool morphologies and plane-bed channels toward pool-riffle morphologies in channels, where average gradients are too steep for these morphologies to occur as a free-formed alluvial structure (Montgomery et al., 1996, 2003).

2.1.4. Model outputs

2.1.4.1. Riparian vegetation. The models described above apply to five potential channel-morphologic groups and incorporate 230 distinct states in eight separate STMs (Table 1). The VDDT provides a non-spatial, pixel-based framework for running STMs. We used 1000 pixels in each of our model runs, conceptualizing these as individual polygons that provided a large number of replicates from which the spatially averaged behavior of the STM could be evaluated. To run an STM, VDDT evaluates the initial state of each pixel in the model, uses a stochastic process to determine if disturbance-driven state transitions occur, tracks the age of each pixel and invokes successional transitions in the absence of disturbance, and then saves the state of each pixel at the end of each annual time step. Initial conditions specifying the proportion of pixels in each state must be supplied, and the simulation results can be queried to output the proportion of pixels in each state at any time step. If simulations are run over a long time with a constant disturbance regime, the proportion of pixels in each state converges on a dynamic equilibrium. Simulations can also track changes in the proportional distribution of states in response to a change in the disturbance regime. Because each state in a STM is defined by the expected characteristics of the riparian vegetation, the proportional distribution of pixels among states can be interpreted as representing the percentage of the riparian zone in

each vegetation state, averaged across all reaches described by the STM.

2.1.4.2. Channel conditions. Fourteen categorical variables were used to describe the expected morphologic characteristics of the stream channel and valley floor. These variables were drawn from the criteria and indicators developed for the Aquatic Riparian Ecosystem Monitoring Program of the Northwest Forest Plan (Reeves et al., 2004), the aquatic and riparian monitoring guidelines developed for the interior northwestern United States (Kershner et al., 2004), and the Environmental Protection Agency, Region 10, stream monitoring guidelines (MacDonald et al., 1991). Variables chosen were (1) bank stability, (2) undercut banks, (3) amount of vegetated streambank, (4) relative amount of shade, (5) channel width relative to free-formed width in undisturbed states, (6) expected dominant streambed sediment in undisturbed states, (7) relative increase in fine-sediment with disturbance, (8) degree of gravel embeddedness; the relative abundance of (9) large wood, (10) pools, and (11) large pools; the amount of (12) pool structure, (13) off-channel habitat, and (14) riffles. The degree to which these physical attributes change with disturbance-forced state transitions depends on the underlying potential channel-morphologic group. We followed Montgomery and Buffington (1998) and Montgomery (1999), assigning relatively small changes in physical attributes to source and transport reaches and assigning much larger changes to response reaches. We also assigned relatively large changes in the abundance of wood-forced pools, large pools, and pool structure with recruitment of large wood to plane-bed and cascade reaches.

The 14 qualitative variables describing channel conditions within each of the 230 states used in the STMs was ranked on a qualitative four-factor scale based on personal experience and available literature. Because the channel condition rankings are tied directly to each state, any change in state resulting from succession or disturbance results in a new suite of rankings. We illustrate the model outputs by examining changes in 4 of the 14 channel-condition variables from a single pixel in the unconstrained step-pool STM undergoing state transitions, first from a wood-poor debris flow and then from large wood recruitment.

Initially, the pixel is in an old-forest state with abundant large wood, riparian hardwoods on the streambanks, and large conifers on the floodplain. The qualitative channel condition rankings for bank stability and shade are high, and large wood and pools are abundant. A debris flow lacking large wood causes a state transition to a channel with little large wood and few riparian hardwoods on the streambanks. In the new state, ranking for bank stability, shade, and pools are all moderate, and large wood abundance is low. The abrupt change in channel conditions with the state transition reproduces the expected channel behavior following an episodic disturbance. Recovery of channel conditions requires a state change, driven either by succession or disturbance, in this case via recruitment of large wood from the floodplain forest, which has a mean reoccurrence interval of 20 years in old-forest states (Table 2). In the new state, qualitative channel condition rankings remain moderate for bank stability and shade, but increase to abundant for large wood and

pools. This abrupt transition for a single pixel is unrealistic as large wood recruitment and channel response to increased wood loading are likely to be gradual. However, in a mid-scale analysis involving a large number of pixels impacted by debris flows, the network averaged response will be smoothed because disturbances, including wood recruitment, occur stochastically, so that some channels will recover quickly and others very slowly.

The STM simulations do not directly output channel condition rankings. Rather, model outputs characterize the proportion of pixels in each state within the model and the change in this distribution through time. Because each state is linked to a set of variables defining the channel condition, the proportional distribution of pixels among states can be interpreted as representing the percentage of the channel length in a given potential channel-morphologic group in a specified channel condition as described by the 14 qualitative variables.

2.1.4.3. Habitat suitability. Channel attributes were linked to habitat suitability for migration, spawning, summer rearing, and winter rearing of chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*). In general, cold water in large pools with cover provided by undercut banks or large wood in relatively large, low-gradient streams provides critical summer migratory habitat for spring chinook salmon, whereas the steelhead migrate upstream in late winter and spawn in spring so that summer migratory habitat is not a critical constraint. Pool tailouts in pool-riffle streams and in plane-bed reaches with a wood-forced pool-riffle structure are preferred spawning habitat for chinook salmon (Montgomery et al., 1999), whereas steelhead can spawn in higher gradient reaches so that riffles in step-pool reaches provide potential spawning habitat. Abundant fine sediment, high gravel embeddedness, and loss of riffles following floods all reduce spawning habitat suitability. Pools and pool-structure, shaded channels with cold water, and abundant riparian hardwoods provide the preferred summer rearing habitat for chinook salmon. Summer rearing for steelhead is similar, but more dependent upon riffle habitat (Hicks et al., 1991). Finally, deep pools with abundant structure, undercut banks, and clean gravels as well as off-channel habitat provide preferred winter-rearing habitat. Loss of pools, pool structure, off-channel habitat, and increased water temperature from decreased shade all decrease habitat suitability for juvenile rearing. We developed a generic habitat template for these species – grouping them together as anadromous salmonids – rather than tailoring habitat suitability indices directly to life-cycle requirements of individual species.

Habitat suitability for four life stages of anadromous salmonids (migration, spawning, summer rearing, and winter rearing) was ranked on a qualitative four-factor scale based on personal experience and available literature. On the basis of the 14-variable qualitative channel condition variables (described above), habitat suitability was ranked as intolerable, tolerable, suitable, and very suitable for each of the 230 states in the models. Habitat suitability rankings, like channel condition rankings, are tied directly to each of the states used in the models, and any change in state results in a new suite of habitat suitability rankings. Thus, any change in state resulting from succession or

disturbance results in a new suite of habitat suitability rankings for each of the four life-stages of anadromous salmonids.

As described above, STM simulations only characterize the proportion of pixels in each state within the model and the change in this distribution through time. The proportional distribution of pixels among states can be interpreted as representing the percentage of the channel length in a given potential channel-morphologic group with a specified habitat suitability for each life stage.

2.2. Example application to the Upper Grande Ronde river

2.2.1. Study site description

The Interior Northwest Landscape Analysis System (INLAS) study area comprises 178,000 ha of the Grande Ronde River subbasin upstream of La Grande, OR (Fig. 1). For the purpose of developing and illustrating the use of aquatic–riparian STMs, we restricted our efforts to a 54,000-ha portion of the Upper Grande Ronde River watershed. The study area contains habitat for chinook salmon and steelhead, both of which are listed as threatened under the Endangered Species Act.

The stream network in the central portion of the Upper Grande Ronde River is dominated by wide valley floors along the Grande Ronde River, Sheep Creek, and Fly Creek. Most of these areas are privately owned and are maintained as wet or dry meadows managed primarily for grazing. These private lands constitute some 7800 ha. The remaining land (46,200 ha) is managed by the U.S. Forest Service. Downstream of the private lands, the mainstem of the Grande Ronde River flows through a narrow canyon; tributaries upstream of the private lands occur in a variety of geomorphic settings, from small, low-gradient streams with wide valley floors dominated by wet meadows, to steep, deeply incised drainages flowing through mid- to high-elevation conifer-dominated forests. Elevations range from 1000 m to over 2400 m along the watershed divide at the headwaters of the Grande Ronde River.

2.2.2. Delineation of the perennial stream network

Our initial efforts to classify the perennial stream network of the Upper Grande Ronde River used the existing line coverage of streams from the 1:24,000 scale digital line graphs available from the Wallowa-Whitman National Forest. However, the sinuosity of channels in the digital stream coverage poorly matched the channels visible on 1:24,000 digital orthophotographs. Consequently, we generated a digital stream network from 10-m DEM data and a geographical information system process that better matched the visible stream network. An ArcGIS script was then used to split the stream network into the channel-gradient classes defined for the potential channel-morphologic groups. Contributing watershed area at the head of each stream reach was calculated with a standard ArcGIS process. We lacked field data from the Blue Mountains for separating perennial stream reaches from intermittent or ephemeral streams. Therefore, we used a threshold value of 50 ha, the average watershed area identified at the limit of discontinuous perennial flow from streams in the mountains of eastern Washington (Palmquist, 2005), an area with climate similar to that of the Blue Mountains.
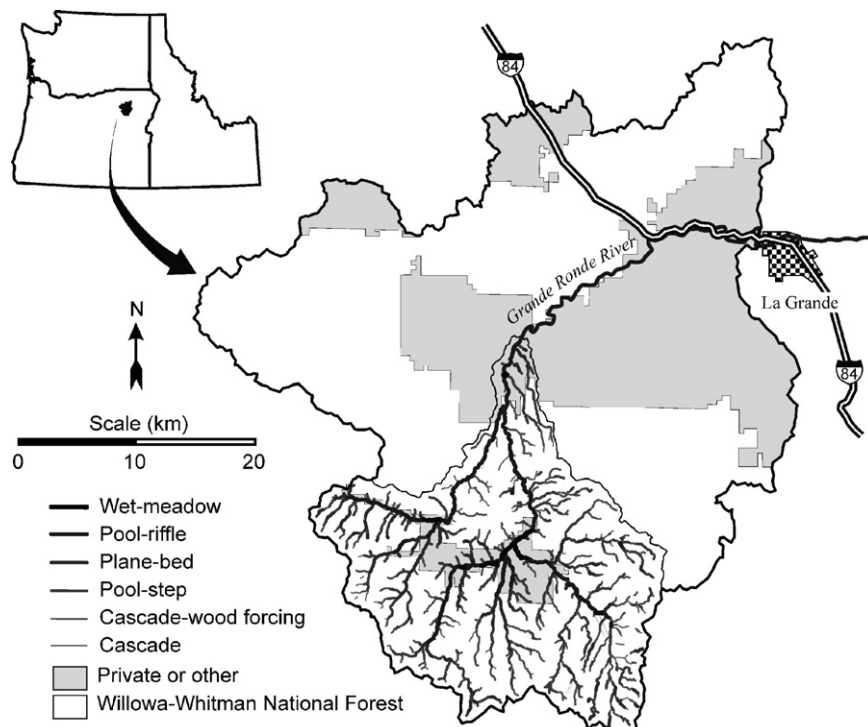

Fig. 1. The Interior Northwest Landscape Analysis System (INLAS) project area showing large blocks of land not managed (shaded) and managed by the U.S. Forest Service. The perennial stream network within the Upper Grande Ronde River watershed is shown.

Each reach of the perennial stream network was classified into a potential channel-morphologic group, using stream gradient and watershed area. We attempted to further classify channel reaches by channel constraint—the ratio of the width of the active channel to the width of the floodplain. The resolution of the 10-m DEM was insufficient to show the actual widths of valley floors and active stream channels. Therefore, we designated the following headwater tributaries as constrained: channels with gradients between 3 and 6.5% and watershed areas less than 400 ha, channels with gradients between 6.5 and 12% and watershed areas less than 800 ha, and all channels with gradients greater than 12%. All other reaches were designated as unconstrained.

2.2.3. Model simulations

Each STM was run to examine the historical condition (ca. 1880) of stream channels and riparian zones in the Upper Grande Ronde River, changes that might have occurred following Euro-American settlement (1880–2000), and the recovery potential (2050). We had no way to specify the initial conditions of riparian polygons for the historical model runs. Therefore, we ran each aquatic–riparian STM with the historical disturbance regimes to generate an equilibrium, historical distribution of states. The distribution appeared to reach a dynamic equilibrium within 500 years, but to make sure, the models were run an additional 2500 years. The ending state, after 3000 years, represented the average conditions that might have existed in 1880, prior to Euro-American settlement. Using the historical distribution as the initial condition, we ran the STMs with the current disturbance regimes for 120 years, outputting the proportional distribution of states after each 10-year interval, to examine the time trend in changes that might have occurred from 1880 to 2000. We then ran the STMs an additional 50 years with the historical disturbance regime to examine the potential for passive restoration to achieve historical conditions by 2050.

Model outputs describing riparian vegetation states are grouped by vegetation structure to expedite presentation of the simulation results. With the exception of a single state in the wet meadow, all pioneer-forb states were grouped together even though they are the starting states for both meadow and forest successional trajectories; wet meadow states – those states with high water tables – dominated by pioneer-forbs, grasses or sedges with or without willows were grouped together as wet meadow states; dry meadow states dominated by grasses with or without willows were grouped together as dry meadow states; and forested states were grouped into stand initiation, stem-exclusion, young-multistrata, and old-multistrata states. We also summarized 4 of the 14 qualitative variables used to rank channel conditions and the habitat suitability rankings for the four life stages of anadromous salmonids. Results are presented for each potential channel-morphologic group and for the fish-bearing portion of the stream network for which we calculated averages weighted by the proportional length of channel in each potential channel-morphologic group likely to support anadromous salmonids.

3. Results

3.1. Wet meadows

3.1.1. Riparian vegetation

About 45% of the areas in the wet meadow potential morphologic group were in wet meadow vegetation states, especially willow-sedge communities, under the historical disturbance regime (Fig. 2A). The remainder of the area was in coniferous forest states because of floods that caused channel erosion, down cutting, and lowered the water table. Most conifer forests were in the stand initiation and stem-exclusion states because of recent wildfires, but about 10% of the area was in young- and old-multistrata forest states (Fig. 2A).

Under the current disturbance regime, wet meadow states were immediately impacted by widespread successional-change grazing. Willows decreased in the first 50 years whereas the Kentucky bluegrass (*Poa pratensis*) and pioneer-forb states increased. Stream channels in these states became more susceptible to bank erosion and down cutting, but since large floods were infrequent, the total area of wet meadows decreased only 10% over 50 years (Fig. 2A). The area of young- and old-multistrata forest conditions increased with fire suppression. Intense grazing by domestic sheep reduced the rate of conifer invasion in areas with incised channels and increased the area in pioneer-forb states. In all, about 80% of the wet meadow potential morphologic group was non-forested after 120 years under the current disturbance regime.

Elimination of successional-change grazing with the return to the historic disturbance regime allowed rapid establishment of conifer seedlings and increased the area in stand-initiation states (Fig. 2A). Areas remaining in wet meadow states were recolonized by sedges and willows within 20 years (Table 3). Recovery of dry meadow or forested states back to wet meadows lagged other changes because these first required infilling of incised channels, which only occurred in older forest states where tree roots stabilize streambanks, and especially where large wood was abundant (Table 2).

3.1.2. Channel conditions

Under the historical disturbance regime, much of the channel was in the willow-sedge state. Channel condition rankings reflected stable streambanks that maintained narrow, deep channels dominated by pools (Fig. 3A). Undercut banks and off-channel habitat were common, but large wood was rare or absent. Floods maintained more than half of the length of these channels in an incised state with decreased bank stability and increased accumulation of fines in the streambed. Channels in the pioneer-forb state had little shade. Conversely, the channels in young- and old-multistrata forest states were heavily shaded and had abundant large wood with frequent, large pools. The large wood, however, also contributed to bank instability and slight widening of the channel.

The current disturbance regime produced major changes in simulated vegetative states with correspondingly large changes in channel conditions. Bank stability decreased rapidly, and approximately 60% of reaches lacked bank stability after 120
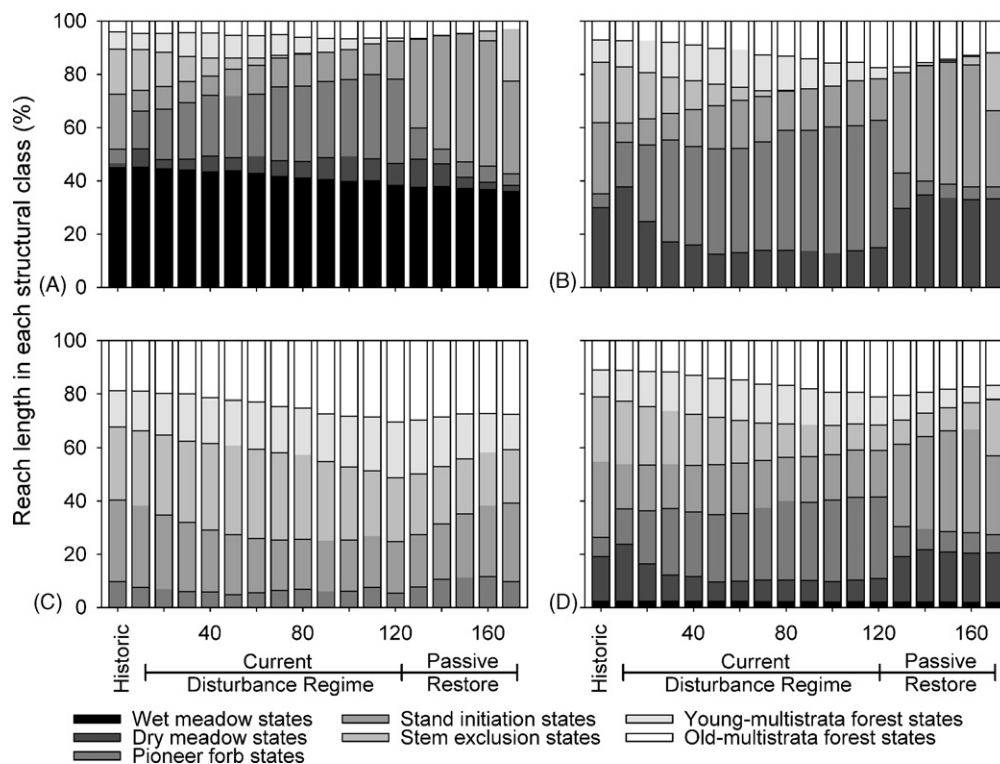
Fig. 2. Changes in the distribution of riparian vegetation over the simulation period. Initial conditions were equilibrium conditions predicted from a 3000-year simulation under the historical disturbance regime (historical, simulation year 0); the changes in structural states over a 120-year period simulated under a current disturbance regime (simulation years 10–120), and then potential recovery after historical disturbance regimes were reinstated (simulation years 130–170). Results are shown for wet meadow reaches (A), pool-riffle and plane-bed reaches (B), step-pool and cascade with wood-forced step-pool reaches (C), and a stream-length weighted average of riparian vegetation states from the fish-bearing portion of the stream network (D).
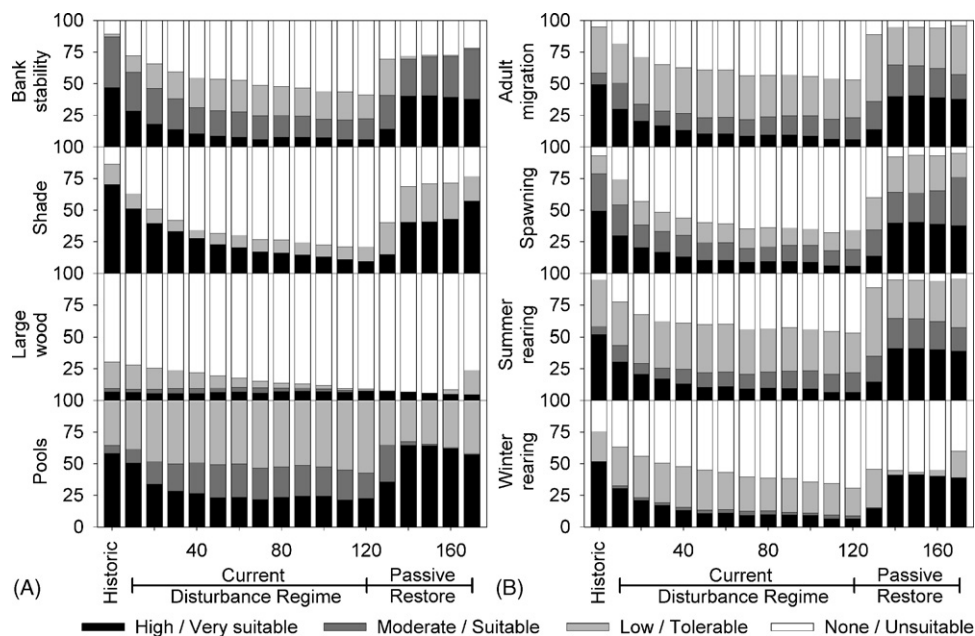
Fig. 3. Relative changes in the percentage of channel length in the wet meadow potential channel-morphologic group ranked on a qualitative four-factor scale for channel condition (A) and habitat suitability for anadromous salmonids (B) over the simulation period. For brevity, only 4 of the 14 channel condition variables are shown. See Fig. 2 for explanation of simulated periods and disturbance regimes.

years (Fig. 3A). The accumulation of fine sediment and the embeddedness of streambed gravels also increased over this period. Changes in vegetative states decreased shade, with nearly 80% of all wet meadow reaches lacking shade after 120 years (Fig. 3A). Because the area in late-successional forest remained relatively constant over the 120 years, the amount of large wood (Fig. 3A) and the amount of structure in pools changed little. However, erosion and aggradation filled some pools and reduced the number of large pools.

Wet meadows recovered rapidly upon return to the historical disturbance regime at simulation year 120. Streambank vegetation increased as did bank stability so that both the amount of fine sediment and gravel embeddedness decreased (Fig. 3A). Also, channels narrowed and the amounts of pool habitat increased. Recolonization and growth of riparian hardwoods, and establishment and growth of conifers increased channel shading.

3.1.3. Salmonid habitat suitability

Historically, channel conditions in the wet meadow morphologic group generally produced very suitable migratory and summer rearing habitat for anadromous salmonids (Fig. 3B). Clean gravels provided high-quality spawning habitat, and off-channel areas provided abundant winter rearing habitat. The simulations also suggested, however, that substantial lengths of these reaches were in less than suitable conditions for anadromous salmonids under historical conditions. Under the current disturbance regime, the percentage in the highest quality habitat declined rapidly, whereas the percentage in unsuitable habitats increased. Spawning habitat was especially impacted with very suitable habitat decreasing to less than 10%, and unsuitable habitat increasing to more than 70%, of all wet meadow reaches by year 120. Habitat suitability improved rapidly with a return to the historical disturbance regime.

3.2. Pool-riffles and plane-beds

3.2.1. Riparian vegetation

These potential channel-morphologic groups have identical riparian forest states and disturbance regimes but exhibit different geomorphic responses to disturbance. Under the historical disturbance regime, wildfire and competing vegetation maintained dry meadows in 30% of these areas (Table 4; Fig. 2B). Riparian hardwoods were present along the channel in more than 85% of these reaches, including in dry meadow and forest states. Stand-replacing wildfires limited the area of young- and old-multistrata forests to approximately 15% of the total area.

Changes to the vegetation were rapid and widespread under the current disturbance regime (Fig. 2B). Most willows and native perennial bunch grasses were lost in the first 30 years, whereas pioneer-forbs increased. Fire suppression increased young- and old-multistrata forests, initially. Grazing by sheep eliminated most conifer regeneration, and caused a large increase in the non-forested area and the eventual loss of stem-exclusion and young-multistrata forests.

The return to a historical disturbance regime reduced grazing and increased conifer seedling establishment in some

pioneer-forb areas (Fig. 2B). Other pioneer-forb areas were recolonized by Kentucky blue grass and then by native perennial grasses and willows. Successional recovery from grazing, however, was much slower than in wet meadows, often requiring at least 40 years for the recovery of bunch-grass dominated dry meadows. Increased rates of stand-replacing wildfire reduced old-multistrata forests while stem-exclusion and young-multistrata forests increased.

3.2.2. Channel conditions

Pool-riffle and plane-bed channel conditions are similar in our models except for the influence of large wood on pool formation; thus, only results for the pool-riffle channels are illustrated (Fig. 4). In pool-riffle channels, where dry meadow vegetation was dense, channels were deep and narrow, and dominated by pools (Fig. 4A). Wildfires kept large areas in early forest successional states so wood recruitment was low, and forced pool-riffle states were uncommon in plane-bed reaches. Heavily shaded channels with abundant large wood comprised about 15% of the reaches. Large wood created more, and larger pools, added substantial cover to existing pools, and also contributed to bank instability and a slight widening of channels. Under the historical disturbance regime, about one-third of these reaches were flood impacted with localized areas of channel erosion or aggradation that reduced bank stability and filled pools.

Under the current disturbance regime, bank stability of pool-riffle channels decreased, the amount of fine sediment and gravel embeddedness increased, and the abundance of pools decreased (Fig. 4A). Pioneer-forb communities became more dominant so that by simulation year 120, nearly 60% of all pool-riffle and plane-bed reaches lacked shade. Small increases in late-successional forest led to small increases in reaches with abundant large wood, which in turn produced pools in plane-bed reaches. These effects were small and were insufficient to offset the loss of previously pool-dominated channels in dry meadow states. Pool-riffle reaches recovered slowly upon return to the historical disturbance regime because of the long period needed for successional recovery of perennial bunch grasses and willows as well as time needed to grow large trees that provide shade and large wood (Fig. 4A).

3.2.3. Salmonid habitat suitability

Anadromous salmonid habitat differed between pool-riffle and plane-bed morphologies. The historical disturbance regime generated abundant migration, spawning, and rearing habitat in pool-riffle reaches with dry meadow vegetation states and in reaches with abundant wood (Fig. 4B). The amount of the highest quality habitat decreased rapidly under the current disturbance regime, accompanied by large increases in unsuitable habitats. Habitat recovery after returning to the historical disturbance regime (Fig. 4B) was much slower than in wet meadow reaches (Fig. 3B).

Plane-bed reaches never provided optimal migration and spawning habitat because few reaches were in the wood-forced pool-riffle state and because the free-formed structure of these channels does not include abundant large pools and spawn-
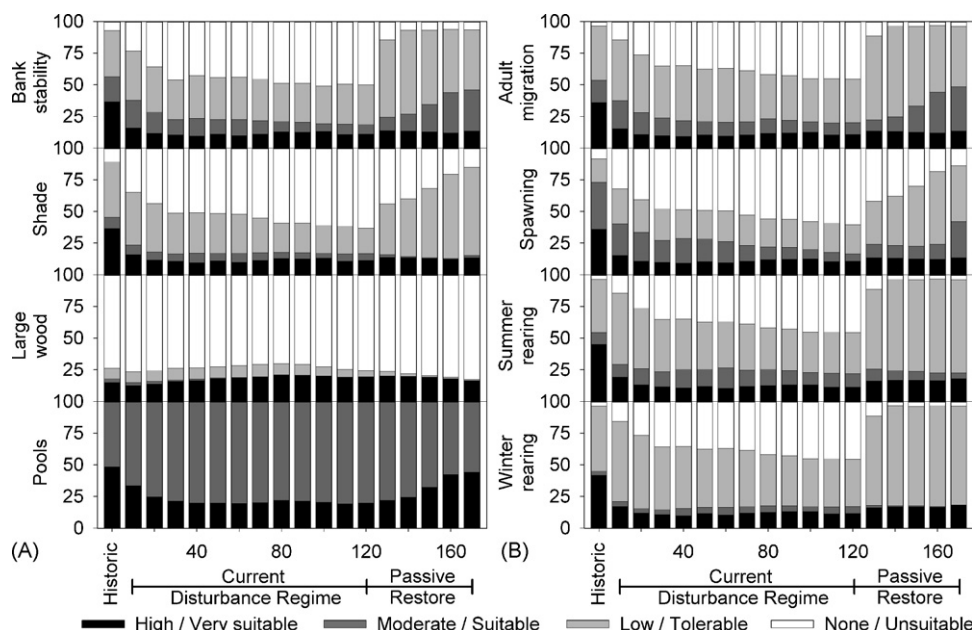
Fig. 4. Relative changes in the percentage of channel length in the pool-riffle potential channel-morphologic group ranked on a qualitative four-factor scale for channel condition (A) and habitat suitability for anadromous salmonids (B) over the simulation period. For brevity, only 4 of the 14 channel condition variables are shown. See Fig. 2 for explanation of simulated periods and disturbance regimes.

ing riffles. Reaches in late-successional dry meadows provided abundant high-quality summer rearing habitat, but lacked off-channel habitat for winter rearing. Habitat quality decreased under the current disturbance regime and recovered slowly after the switch back to the historical disturbance regime.

3.3. Step-pools and cascades

3.3.1. Riparian vegetation

The STMs for the unconstrained and constrained free-formed step-pools, cascades with wood-forced step-pools, and cascades all shared similar riparian forest states and disturbance regimes, which resulted in identical riparian vegetation trajectories in our simulations. Under the historical disturbance regime, young- and old-multistrata forests occupied between 25 and 30% of the area (Fig. 2C). The constrained reaches had slightly less old forest because debris flows are stand-replacing disturbances over the full width of the valley floor. In addition, shading from adjacent upland forest yielded fewer reaches with riparian hardwoods in constrained than in unconstrained reaches.

Fire suppression under the current disturbance regime (Table 2) increased the area in old forests with a concurrent increase in snags (Fig. 2C). Heavy grazing rapidly decreased riparian hardwoods along stream channels. But unlike in the large meadow systems, grazing was never sufficient to suppress conifer establishment.

Riparian hardwoods increased rapidly in both the unconstrained and constrained reaches with the return to the historical disturbance regime. The increase in stand-replacing wildfire led to a gradual loss in young- and old-multistrata forests with a con-

cordant increase in the areas in pioneer-forb and stand-initiation states (Fig. 2C).

3.3.2. Channel conditions

The abundance of large wood was the biggest factor influencing channel structure (Figs. 5A and 6A), especially in the cascade channels with wood-forced step-pools. Under historical conditions, 60% of the reaches were in stem-exclusion or later-successional forest states, so large wood and pools were abundant and channels were well shaded (Figs. 5A and 6A). The current disturbance regime produced only minor changes. Heavy grazing led to some decreased bank stability, channel widening, and increased abundance of fines. The amount of old forests and therefore the abundance of wood-formed pools increased gradually. Return to the historical disturbance regime resulted in regrowth of riparian hardwoods and increased bank stability and shade within the first decade. Over the following decades, increased wildfire not only increased wood recruitment but also increased area in pioneer-forb states with reduced shade and bank stability (Figs. 5A and 6A).

3.3.3. Salmonid habitat suitability

Step-pool reaches were near the upper gradient limits for adult migration and holding of anadromous salmonids and generally lacked riffles with appropriate sized-gravels for spawning (Fig. 5B). Cascade reaches were even higher gradient and were generally unsuitable salmonid habitat, even in a wood-forced step-pool state (Fig. 6B). Step-pool channels under the historical disturbance regime had abundant large wood and abundant pools that provided highly suitable summer and winter rearing habitat (Fig. 5B), whereas this habitat was present, but of more limited
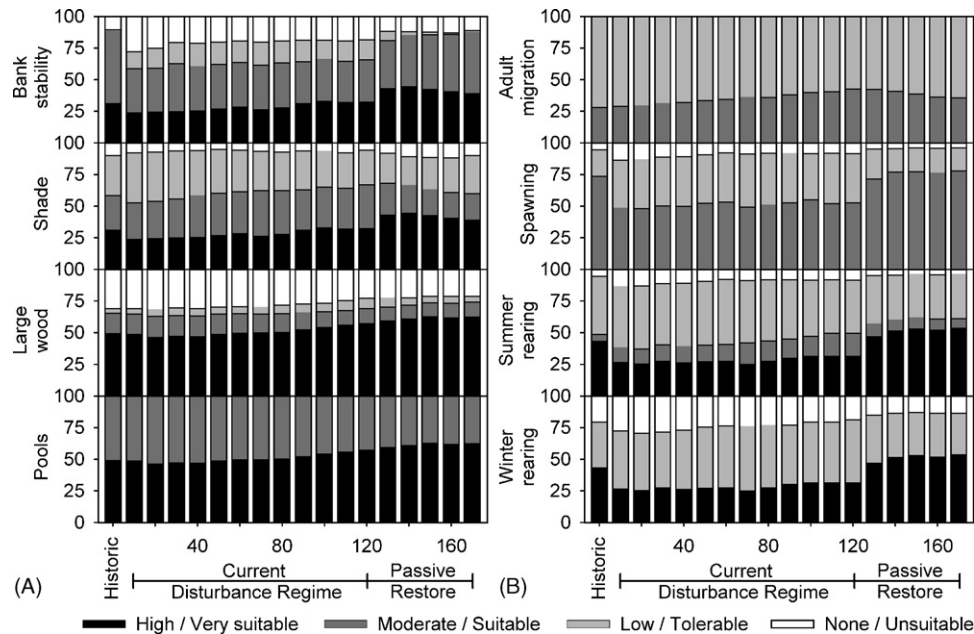
Fig. 5. Relative changes in the percentage of channel length in the step-pool potential channel-morphologic group ranked on a qualitative four-factor scale for channel condition (A) and habitat suitability for anadromous salmonids (B) over the simulation period. For brevity, only 4 of the 14 channel condition variables are shown. See Fig. 2 for explanation of simulated periods and disturbance regimes.

quality in the cascade reaches (Fig. 6B). Summer and winter rearing habitat quality decreased within the first decade under the current disturbance regime (Fig. 5B), after which increased abundance of large wood and pools led to gradual increases in the amount of suitable and very suitable rearing habitat (Fig. 5B) that persisted for more than five decades after the switch back to the historical disturbance regime in simulation year 120.

3.4. Summary of changes to the fish-bearing stream network

Only 40% of the stream network (watershed areas greater than 500 ha and reach gradients less than 12%) is likely to support fish. Here, we combined all fish-bearing reaches with a length-weighted average to summarize network-wide changes in
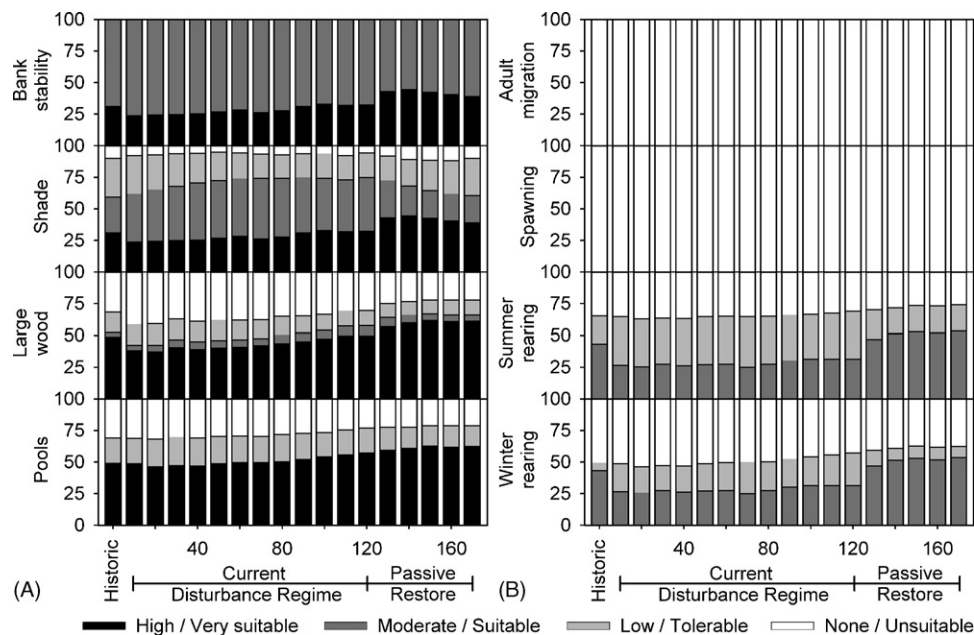

Fig. 6. Relative changes in the percentage of channel length in the cascade with wood-forced step-pool potential channel-morphologic group ranked on a qualitative four-factor scale for channel condition (A) and habitat suitability for anadromous salmonids (B) over the simulation period. For brevity, only 4 of the 14 channel condition variables are shown. See Fig. 2 for explanation of simulated periods and disturbance regimes.

riparian vegetation and channel conditions that influenced habitat for anadromous salmonids within the Upper Grande Ronde River.

3.4.1. Riparian vegetation

Under historical conditions, meadows and late-successional forests each comprised nearly 20% of the riparian vegetation along the stream network and only small areas were in the pioneer-forb state (Fig. 2D). Heavy grazing under the current disturbance regime produced rapid decreases in riparian hardwoods and a gradual decrease in late-successional dry meadow vegetation states. Grazing by sheep suppressed conifer establishment in meadows that occupied wide valley floors along large streams and led to large areas maintained as pioneer-forbs. This reduced numbers of developing stands that eventually reduced the area in stem-exclusion and young-multistrata forests. At the same time, fire suppression increased old-multistrata forests. Rapid changes followed return to the historical disturbance regime. The area in riparian hardwoods and in both dry meadow and stand-initiation states increased rapidly, whereas pioneer-forb states decreased. More frequent wildfires gradually decreased the amounts of young- and old-multistrata forest, whereas the increase in stem-exclusion forests lagged the change back to the historical disturbance regime by 50 years (Fig. 2D).

3.4.2. Channel conditions

The models simulated large changes in channel conditions over the entire fish-bearing stream network under the current disturbance regime, relative to the historic conditions (Fig. 7A). Disturbances destabilized streambanks, leading to loss of undercut banks, channel widening, accumulation of fines, and increased embeddedness of streambed gravels. For example, the percentage of the stream network ranked as having high or moderate amounts of fine sediment increased from less than 15% historically to 50% by year 120. Also, the percentage of the stream network lacking shade increased from 10% to just over 40% in 120 years (Fig. 7A). Initially, pools were lost from meadow reaches as stream width increased owing to destabilization of streambanks from grazing. But fire suppression increased late-successional forest area as well as large wood recruitment so that the percentage of the stream network with abundant pools gradually increased (Fig. 7A).

3.4.3. Salmonid habitat suitability

Under the historical disturbance regime, approximately, 40% of the fish-bearing stream network was ranked suitable or better for migration of adult salmonids, whereas 60% was suitable for spawning (Fig. 7B). However, the area ranked as very suitable was quite small and concentrated in pool-riffle, and to a lesser extent, wet meadow reaches (Figs. 3B and 4B). Pool-riffle reaches made up approximately one-third of the fish-bearing stream network, and historically, only about 35% of these reaches were in the highest quality habitat conditions at any given time. Rearing habitat for juveniles was distributed across a much wider array of stream types within the stream network, and the amount of habitat ranked as very suitable ranged between 35 and 40% (Fig. 7B).

The amount of suitable and very suitable habitat decreased immediately under the current disturbance regime. The amount of habitat ranked as unsuitable for spawning and winter rearing exceeded 45% after 120 years (Fig. 7B). Network-wide recovery of high-quality rearing habitat was rapid after return to the historical disturbance regime, but adult migration and spawning habitat recovered much more slowly (Fig. 7B).
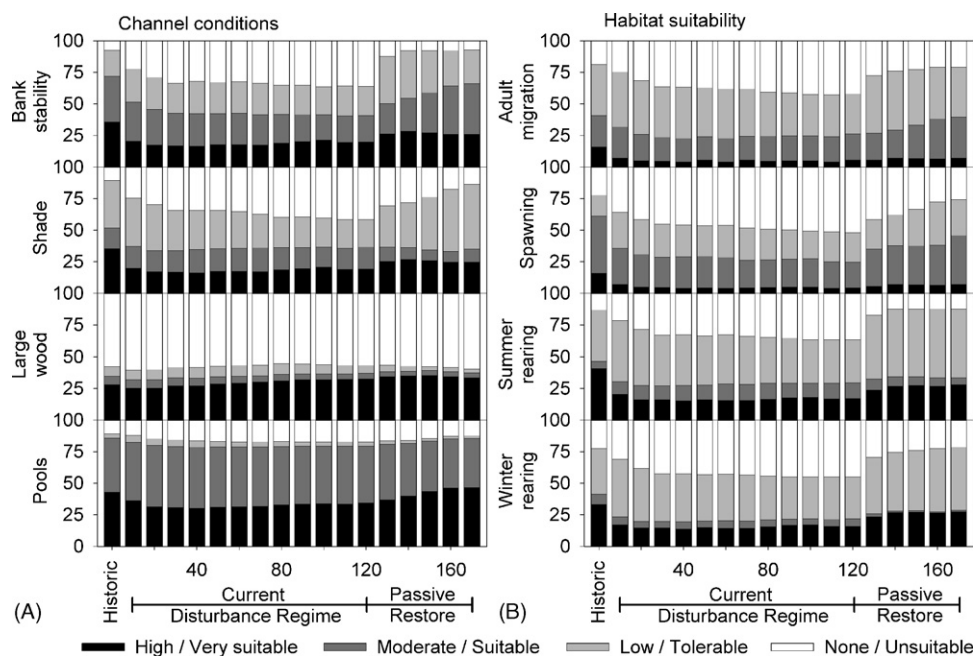

Fig. 7. Relative changes in the percentage of channel length, averaged over the fish-bearing portion of the stream network, ranked on a qualitative four-factor scale for channel condition (A) and habitat suitability for anadromous salmonids (B) over the simulation period. For brevity, only 4 of the 14 channel condition variables are shown. See Fig. 2 for explanation of simulated periods and disturbance regime.

4. Discussion

4.1. Results of model simulations

The wet meadow potential morphologic group is a minor component of the stream network in the Upper Grande Ronde River but is important in management considerations because it constitutes the preferred spawning locations for chinook salmon within the watershed. Our simulations showed that grazing rapidly converted most of the willow-sedge domi-nated wet meadows to bluegrass or pioneer-forb states with high water tables. Channel incision in grazed wet meadow states was gradual, however, because major floods were rare (Fig. 2A). With the cessation of grazing, most wet meadow states returned to willow-sedge dominance within two decades. Thus, our model simulations suggested that passive restora-tion would be rapid and effective in this potential morphologic group (Fig. 3). These simulation results seem reasonable given the rapid changes in vegetation composition and structure in lightly grazed wet meadows following disturbance by beaver or major floods (Hall, 2005) and rapid regrowth of estab-lished willows with removal of grazing (Brookshire et al., 2002).

Similar to wet meadows, grazing caused rapid changes in the pool-riffle potential morphologic group (Fig. 4). The mod-els simulated a rapid decrease in reaches with abundant pools as channels get wider and shallower. Pool frequency was never less than moderate, however, because these reaches had a free-formed pool-riffle structure. These and other changes in channel condition assigned to grazing-related transitions seem reason-able given that intense grazing decreases bank stability, increases deposition of fines within the streambed, and increases embed-dedness of streambed gravels (Kauffman et al., 1983a; Kauffman and Krueger, 1984; Trimble and Mendel, 1995).

The pool-riffle STM was structured so that successional recovery of dry meadows would be relatively slow (Table 4), requiring 20 years, on average for the transition from pioneer-forb communities to blue-grass dominated meadows, and an additional 30 years to transition to a native grassland with scat-tered willows. Cessation of grazing rapidly improved habitat from unsuitable to tolerable as riparian vegetation recovered from the pioneer-forb state into early-successional meadow grasslands and began to stabilize streambanks. Such rapid recov-ery of vegetation is consistent with the results of many exclosure studies (Kauffman et al., 1983b; Kondolf, 1993; Platts and Rinnie, 1985). Recovery of channel conditions is expected to lag that of riparian vegetation (Kondolf, 1993), but few data are available to determine the time required for channel read-justment. Several exclosure studies have documented channel narrowing, increased depth and decreased width:depth ratios (Clifton, 1989; Magilligan and McDowell, 1997), but channel responses summarized by McDowell and Magilligan (1997) showed no trend of increasing channel recovery with time since exclosure. Other studies document no change in measured channel attributes, even after several decades (Kondolf, 1993). Additional studies will be needed to resolve rate of recovery of both channel condition and habitat suitability under pas-sive restoration and to identify the activities that could speed restoration.

We initially assumed that dry meadows were maintained by frequent fires under the historical disturbance regime. Early model runs, however, showed that less than 10% of pool-riffle channels were in dry meadow vegetation. Historical documen-tation of riparian vegetation in the Blue Mountains is poor, although a few photographs taken in the early 1900s (Skovlin and Ward Thomas, 1995) suggest that meadows were common along wide valley floors. Assuming that competition from grasses and shrubs might have limited conifer regeneration, we decreased the annual probability of conifer establishment from 0.068 to 0.01. The revised models better match the assumed historical distribution of meadows.

Initial model runs under the current disturbance regime resulted in near complete loss of dry meadows. Grazing decreased competitive exclusion of conifers, whereas fire sup-pression increased survival through the stand initiation stage, resulting in wide-scale transition of meadows to forests. These results disagreed with present day observations showing that non-forest vegetative states (meadow and pioneer-forb) com-prise nearly 50% of the riparian areas along wide, low-gradient channels. Clearly, our models were missing critical processes controlling presence of dry meadows. For example, conifer seedlings are susceptible to spring grazing by sheep and to cold air drainage and frost kill without a protective overstory canopy. Alternatively, conifers may have been intentionally cleared from some wide valley floors to improve forage production or to man-age meadows for cutting hay (Vavra, personal communication, Pacific Northwest Research Station, La Grande, OR). Sheep grazing has been intense throughout much of the Blue Mountains (McIntosh et al., 1994; Skovlin and Ward Thomas, 1995), so the models were restructured to allow grazing-driven transitions from stand initiation states back to pioneer-forb communities under the current disturbance regime. With this modification, the amount of non-forest area predicted by the model more closely matched the current vegetation.

Channel conditions of three potential channel-morphologic groups are sensitive to loading of large wood—the plane-bed, step-pool, and low-gradient cascades with wood-forced step-pool morphology. Plane-bed channels in a wood-forced pool-riffle state can provide spawning habitat for anadromous salmonids (Montgomery et al., 1999), and because these chan-nels are common in the Upper Grande Ronde River watershed, they can substantially affect the total amount of spawning habitat available (Table 1). Step-pool channels are important for all life stages of resident salmonids (Magee et al., 1996; Montgomery et al., 1999) and provide rearing habitat for anadromous salmonids. Although pools are a free-formed component of these channels, many studies have shown that pool abundance increases where large wood is present, and that pools are both larger and have more structure (Buffington et al., 2002). The abundance of pools is usually highly correlated with juvenile salmonid abundance (Latterell et al., 2003). Finally, cascade channels seldom sup-port fish because pools and other slow water habitats are rare. However, large wood can force lower gradient cascade channels into a step-pool structure, and can even create pools in higher

gradient cascades so that trout can be found in channels with average gradients in excess of 20% (Latterell et al., 2003).

Our models simulate only small changes in channel conditions in the step-pool and the cascade with wood-forced step-pool morphologic groups under the current disturbance regime (Figs. 5 and 6). Further, passive restoration results in immediate recovery of habitat suitability, with the percentage of channel length in these morphologic groups ranked suitable or very suitable for all life stages of anadromous salmonids exceeding that of the historical condition. However, these results for the step-pool and the cascade with wood-forced step-pool morphologic groups are likely unrealistic because of simplifying assumptions made when developing the models.

To simplify model development, we excluded a number of disturbances known to affect stream networks and riparian forests, including forest harvest and removal of large wood from stream channels. Although these activities are now uncommon in riparian zones on national forest lands in the interior Columbia River basin, forest harvest, at least, was common in the past, especially along wider, low-gradient valleys because of the relative ease of human access (Hessburg and Agee, 2003; McIntosh et al., 1994; Wissmar et al., 1994). Also, splash-damning was used to transport logs in the Upper Grande Ronde River. It is likely that land-use activities in the Upper Grande Ronde River watershed have dramatically reduced the amount of large wood in stream channels as well as the area of riparian zones with old-multistrata forests. Additionally, we did not include the effects of roads, despite considerable evidence that poorly built or poorly maintained roads are a major source of fine sediment to streams (Trombulak and Frissell, 2000) and are closely linked to declines in native fish populations (Lee et al., 1997). Thus, we expect these models under predicted the extent of change in channel conditions and habitat suitability under the current disturbance regime. Further, we expect that a passive restoration strategy would result in much delayed recovery—first requiring regrowth of old-multistrata forests followed by recruitment of large wood.

Simulation results summarized for the fish-bearing portion of the stream network are driven by the response of the pool-riffle and step-pool morphologic groups because these are the dominant channel types (Table 1). Migratory and spawning habitat is primarily located in pool-riffle channels lower in the stream network. Recovery of channel conditions and habitat suitability with passive restoration in the dry meadow states is relatively slow and reflected in the slow increase in the length of stream channel ranked as very suitable for these life stages (Fig. 7). Rearing habitat is more evenly distributed among pool-riffle and step-pool morphologic groups. The rapid decline in the length of channel ranked very suitable for rearing habitat reflects changes for both morphologic groups. Little recovery is predicted in pool-riffle channels with passive recovery so the rapid increase in the length of channel ranked very suitable results primarily from changes in step-pool channels.

Overall, our simulation results disagree with results of long-term stream surveys in the interior Columbia River basin. McIntosh et al. (2000) documented a continued decline in the number of large pools in the Grande Ronde River from reaches originally surveyed between 1934 and 1942 and resurveyed

between 1990 and 1992. Resurveys also showed that fine sediment and gravel embeddedness were high, and that amounts of large wood were approximately half that expected for rivers where human land-use impacts were minimal (McIntosh et al., 1994). These data suggest that land-use activities in the Upper Grande Ronde River watershed have had greater impacts on channel conditions and habitat suitability than we simulated, probably because effects of several land-use practices have yet to be addressed in our models. These include the direct effects of forest harvest and removal of large wood from stream networks, erosion and stream sedimentation from road networks, splash-damning to transport logs, beaver trapping, and dredge mining. Neither did we include the potential effects of thinning and fuels reduction treatments when projecting future conditions of channels and riparian forests. We expect that recovery under a passive restoration strategy would be much slower than simulated, both because current conditions are worse than predicted and because we overestimate the riparian area in old-multistrata forest.

4.2. Utility of the state and transition modeling approach

Our models provide a template for describing changes in riparian vegetation and channel condition that occur through vegetative succession and disturbances. Although the use of STMs in upland ecosystems is well documented, their use in riparian and aquatic systems is novel, even though the conceptual underpinnings exist in the geomorphologic literature and stream classification schemes. Our models are not predictive, in the sense that they neither simulate basic physical mechanisms nor predict riparian vegetation states or channel conditions from simulated physical processes. Rather, these are rule-based models. Therefore, model outputs reflect the modelers' understanding of system properties and interrelationships—to the extent that these can be captured within the model structure. Our results suggest that the STM approach may be a useful way of organizing information and knowledge and of projecting expected responses of riparian systems and associated aquatic habitats.

One major limitation of our approach is that the models are not spatially explicit. They simulate hypothetical stream reaches affected by a variety of disturbances but do not link these reaches into a dynamic stream network in which disturbances can propagate downstream. In addition, the stream reaches are not spatially connected to adjacent uplands so that upland disturbances, such as fire, cannot propagate into riparian areas. Consequently, the models do not capture temporal synchrony of many large-scale disturbance events that might affect large portions of the stream network at any given time. The approach, however, provides the building blocks for constructing such a dynamic landscape and network model. Fonnesbeck (2006) demonstrated a possible approach to building a dynamic network model, but his results were dramatically different than ours, most likely because of problems in translating non-spatially explicit disturbance probabilities into spatially explicit disturbance events. For example, in Fonnesbeck's model, most of the landscape is in old, multistrata forest under the historic disturbance regime (Fonnesbeck, 2006; Fig. 4). However, fires were common, historically, and

prevented accumulation of substantial land area in old forest types (Hemstrom et al., 2006). This contrast between results suggests that stand-replacing wildfires are under-represented in Fonnesbeck's model (2006). Clearly, changing the model structure to simulate a dynamic network will not be trivial, requiring additional information on the spatial extent of each disturbance and substantial effort error-checking model parameterizations and conducting sensitivity analyses to ensure that spatial and non-spatial versions of the models provide similar occurrence probabilities for each disturbance event.

These models suffer from difficulties with model parameterization and validation. First, little information exists to quantify disturbance probabilities or the frequency distribution of disturbance sizes, thus we often had to rely on expert opinion. For example, recurrence intervals for wildfires (Hemstrom et al., 2006) and major floods are reasonably well known, whereas little is known about the frequency of debris flows in this landscape despite the fact that over long periods, debris flows may dominate sediment budgets of many watersheds (Kirchner et al., 2001). Similarly, few data are available for estimating hydro-geomorphic recovery of channels following the removal of successional-change grazing across the variety of reach types simulated. The current vegetation can be mapped from aerial photos or from ground-based surveys, but information about past conditions and disturbances is usually anecdotal or missing, making model projections impossible to validate. Clearly, if the model simulations fail to reproduce the current distribution of vegetative states, the model must be wrong. But the converse is not necessarily true. Model outputs that reasonably simulate existing conditions do not validate the underlying model structure.

Despite their limitations, STMs have become popular tools for examining the relationships in complex systems and have now been applied in several large- to mid-scale landscape analyses (Hann et al., 1997; Hemstrom et al., 2001). To date, these landscape–scale analyses have focused on upland vegetation and could not include riparian areas because of their relatively small size and linear-network structure. The riparian–aquatic STMs presented here remain under development, and require more complete treatment of the effects of land-use practices and a modeling framework that allows the STMs to be stitched together in a dynamic stream network. Once a more complete version of the models is available, they can be integrated into the larger analytical structures currently being used to evaluate management effects at both large- and mid-scales within the interior Columbia River basin. At that point, model analyses, including both simulations to project future conditions and sensitivity analyses, will contribute toward illustrating the potential impacts of land-use practices on future conditions of streams and riparian zones within the interior Columbia River basin.

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