RIPARIAN VEGETATION COMMUNITIES OF THE AMERICAN PACIFIC NORTHWEST
ARE TIED TO MULTI-SCALE ENVIRONMENTAL FILTERS[†]N. HOUGH-SNEE^{a,b,*}, B. B. ROPER^{b,c}, J. M. WHEATON^{b,d} AND R. L. LOKTEFF^{a,b}^a *PIBO Effectiveness Monitoring Program, USDA Forest Service Forest Sciences Laboratory, Logan, Utah, USA*^b *Department of Watershed Sciences, Utah State University, Logan, Utah, USA*^c *Stream and Aquatic Ecology Unit, USDA Forest Service Forest Sciences Laboratory, Logan, Utah, USA*^d *US and Intermountain Center for River Restoration and Rehabilitation, Utah State University, Logan, Utah, USA*

ABSTRACT

Riparia surrounding low-order streams are dynamic environments that often support distinct biodiversity. Because of their connection to nearby uplands, riparian vegetation communities at these streams respond to many environmental filters—climatic, physical, chemical or biotic factors—that restrict what species can occur at a given location from within larger regional species pools. In this study, we examined how environmental filters originating at the landscape, watershed and reach scales correspond to riparian plant community composition across the interior Columbia and upper Missouri River basins, USA. We correlated riparian vegetation to environmental filters, identified unique communities and partitioned the variance within riparian vegetation data among filters originating at different scales. Riparian vegetation composition was strongly correlated to landscape-scale filters including elevation, precipitation and temperature. Watershed-scale filters such as grazing and reach filters indicative of fluvial setting were also correlated to vegetation composition, often differentiating communities with similar landscape settings. We identified 10 distinct vegetation communities. Forested communities occurred at higher elevation, moderate gradient reaches with high mean annual precipitation. Shrub–forb systems corresponded to fluvial and watershed disturbances and occurred within climates that could preclude forest establishment. Meadows corresponded to high water tables and/or high grazing activity. Variance partitioning showed that landscape-scale filters explained the most variance within vegetation communities. Global change will alter many of the environmental filters that drive vegetation. Vegetation change may occur rapidly if local filters (e.g. fluvial process) change rapidly or may occur more slowly if larger-order filters (e.g. climate) change slowly and without influencing local hydrogeomorphic filters. By identifying filter–vegetation relationships at large spatial scales, hypotheses can be constructed on how riparian vegetation communities may change under future environmental conditions. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS: riparian ecology; riparian vegetation; environmental filters; assembly rules; Columbia River Basin

Received 14 January 2014; Revised 1 July 2014; Accepted 8 July 2014

INTRODUCTION

Riparian plant communities assemble by passing through diverse environmental filters that restrict what species assemblages can occur at a given site from those species available within larger regional species pools. Environmental filters are processes, natural or otherwise, that can limit the potential biological community of a given site (Tonn, 1990; Keddy, 1992; Grime, 1977). Environmental filters have also been defined as any non-random process or ecosystem attribute that shapes plant community composition, structure or growth (Díaz *et al.*, 2007). Under the latter definition, any process that limits biological community assembly is an environmental filter (Grime, 2001; Díaz *et al.*, 2007). Within riparia, geomorphic and hydrologic processes (Bendix and Hupp, 2000), biotic interactions

(Andersen and Cooper, 2000), regional climate and anthropogenic disturbance serve as filters that shape the composition and structure of vegetation communities (Decamps, 1993; Hupp and Osterkamp, 1996). These processes filter plant communities from regional to local scales by excluding species that are not sufficiently adapted to survive, grow and reproduce under local environmental conditions (Figure 1).

At broad scales, physiographic or climate-regulated environmental conditions such as precipitation, temperature and solar radiation affect plant establishment, growth and survival. Broad-scale climatic filters interact with local geology, hydrology and soils that affect plant physiological and morphological properties to further constrain plant community assembly (Keddy, 1992). Fluvial processes such as overbank flooding, wetland soil formation, flow regimes and sediment deposition and erosion also filter riparian vegetation across numerous plant life stages, including propagule dispersal, seedling establishment, growth and reproduction (Shafroth *et al.*, 2002; Van Pelt *et al.*, 2006; Naiman *et al.*, 2010; Goebel *et al.*, 2012). The filters that

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Figure 1. A schematic representation of the hypothesized relationships between riparian vegetation and landscape-scale, watershed-scale and stream-scale environmental filters. Filters work in a ‘top-down’ fashion to shape plant communities, excluding species and functional groups incapable of responding to stressors at a given site. For example, landscape level variables such as geology, climate and topography prevent certain species from colonizing a region. The remaining species are further filtered by watershed physical properties and stream-scale hydro-geomorphic attributes. Filtering results in vegetation communities suited to local conditions and indicative of local climate, disturbance histories and so forth. At the stream reach scale, vegetation often interacts with hydrology and geomorphology to influence stream channel form.

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shape riparian vegetation depend on a supporting stream’s landscape position, the watershed setting within that landscape, and how landscape and watershed processes interact to conduct water and sediment through stream networks (Figure 1).

Low-order streams connect uplands to stream channels and their associated riparian vegetation and are often tightly coupled to their surrounding watershed. Accordingly, human activities may disproportionately filter low-order stream

riparian plant communities through direct (e.g. timber harvest and rangeland use; Dalldorf *et al.*, 2013) and indirect effects (e.g. spreading invasive species and global climate change). These anthropogenic filters shape riparian vegetation alongside broader-scale climatic, geomorphic and hydrologic processes that can influence stream channel attributes. Although the riparian vegetation of low-order streams must pass through more diverse filters than larger rivers, most studies of riparian vegetation-environment relationships in small streams have only examined how specific disturbances influence vegetation (Rheinhardt *et al.*, 1998). The scale of inference in these disturbance-specific small-scale studies is limited to the limited spatial extents at which sampling occurs (Brierley *et al.*, 2006).

By concurrently examining natural and anthropogenic filters from multiple spatial scales, it may be possible to disentangle the relative effects of landscape-scale, watershed-scale and reach-scale processes on riparian vegetation. Although there have been numerous studies that examine the effects of stream-scale or catchment-scale hydrogeomorphic processes on riparian vegetation (Chambers *et al.*, 2004; Hagan *et al.*, 2006; Stollack and Naiman, 2010; D'souza *et al.*, 2012), no study has elucidated patterns in riparian vegetation community assembly owing to multi-scale environmental filters at sub-continental scales (Richardson and Danehy, 2007). By highlighting vegetation-environment relationships at the multiple scales from which filters originate, riparian vegetation can be linked to multiple processes, from regional climate to watershed physical attributes and local fluvial processes (Richardson and Danehy, 2007). To

disentangle what processes correspond to riparian vegetation, we examined relationships between multi-scale environmental filters and riparian vegetation across the United States' interior Columbia River and upper Missouri River basins. These basins are both targeted for riparian and instream restoration to recover salmonid populations. By examining how riparian communities assemble in response to environmental filters within these basins, watershed managers may better understand the processes responsible for current riparian conditions and set realistic expectations for potential restoration outcomes.

Here, we take a filter-based approach to assess how low-order streams' riparian vegetation communities assemble across the American interior Pacific Northwest. To do this, we asked three questions: (i) Do stream ecosystems of the interior Columbia River and upper Missouri River basins have distinct riparian plant communities? (ii) Do environmental filters and instream habitat attributes differ between vegetation communities? (iii) What environmental filters are most correlated with riparian vegetation composition—landscape-scale, watershed-scale or stream-scale filters?

MATERIALS AND METHODS

Study watersheds

America's interior Columbia and upper Missouri River basins (Figure 2) have extensive headwaters that provide habitat to numerous threatened and/or endangered aquatic species. From 2009 to 2011, we sampled 720 stream reaches

Figure 2. Sampled stream reaches within the interior Columbia and upper Missouri River basins between 2009 and 2011. All riparian monitoring sites were along low-order and low-gradient streams that flow through federally owned or federally managed lands. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

within the interior Columbia and upper Missouri River basins using a spatially balanced, probabilistic sampling design (Kershner *et al.*, 2004). Reaches were low-gradient sites ($\approx 3\%$) on federal lands within subwatersheds [US Geological Survey (USGS) sixth-order Hydrologic Unit Code] with $>50\%$ federal ownership, usually managed by the United States' Bureau of Land Management (BLM) or USDA Forest Service (USFS). American federal lands usually occur high in watersheds and, depending on the management unit, are often managed for natural resource purposes such as cattle grazing or timber harvest and usually have significant road infrastructure to support this management. The physical setting and management legacies of small watersheds, such as those within the study area, may interact with environmental gradients to influence riparian habitats. The environmental attributes of the sampling area are summarized in Supporting Information Table S1.

Environmental, stream and vegetation data

We hypothesized that environmental filters affecting riparian vegetation originate at three main scales: the landscape, watershed and stream reach (Supporting Information Table S1). A scale-based approach to grouping explanatory variables was appropriate because it allowed us to look at the proportion of variance explained by sets of environmental filters at each scale. Landscape filters were those that occur as a result of broad spatial-scale processes: climate, topography and regional geology. We combined stream buffer filters (attributes measured within a 90-m buffer of the stream network) and watershed filters into a single group (herein watershed filters). Watershed filters encompass edaphic properties, physical characteristics and management-related parameters known to affect instream and riparian condition (Nilsson *et al.*, 1994; Ferreira and Moreira, 1999; Chambers *et al.*, 2004; Chessman and Royal, 2004). We identified stream reach-level filters as physical attributes that correspond to streamflow, overbank flooding disturbance and wetland soil development. Stream bankfull width, sinuosity, hydraulic radius, wetted width–depth ratio, gradient, instream wood, bank stability and sediment size all result from hydrogeomorphic processes and interact with vegetation by shaping riparian microclimates where plants establish. Stream attributes not only shape riparian niches available for plant colonization, but they also respond to vegetation composition and structure and influence aquatic habitat (Figure 1).

We aggregated all remotely sensed landscape-scale and watershed-scale filter data within GIS. We used PRISM data (PRISM Climate Group, Oregon State University) to estimate the 30-year average temperature and precipitation within watersheds above each sampled reach between 1980 and 2010 and to estimate precipitation at each reach during the water year in which it was sampled. We estimated

the proportion of each watershed that was composed of igneous, metamorphic, sedimentary or unconsolidated rock (USGS, 2005). Elevation corresponds to climatic, physiographic (Daly *et al.*, 1994) and solar radiation gradients (Goodale *et al.*, 1998), so minimum, maximum and average watershed elevations were derived from 10-m digital elevation models (USGS national elevation dataset). Geographic coordinates were incorporated into the landscape-scale filters to account for unexplained spatial variability. Sample year was used as a proxy for interannual differences in climate or disturbance (Supporting Information Table S1).

We used USFS and BLM grazing allotment data to calculate the proportion of the riparian buffer and watershed that had been grazed by livestock in the last 30 years. Because forests serve as corridors for propagule dispersal following disturbance and tree canopies shape understory light and humidity, we identified the proportion of each watershed and reach covered by overstory forest vegetation using LANDFIRE (USGS, 2012). We also used LANDFIRE data to estimate the proportion of each watershed that had burned between 1997 and 2007. We calculated road density (km/km^2) within each buffer and watershed because roads serve as plant dispersal vectors and alter local hydrology. We used 10-m digital elevation models to calculate watershed area, stream density and the average slope of the watershed and buffer surrounding each reach. An erosivity index—a unitless, continuous measure of the uniaxial compressive strength of lithology types—was calculated to estimate the relative erosion potential at each reach (Cao *et al.*, 2007). Average soil thickness and depth to the seasonal high water table, indicators of hydric soils, were estimated at each reach (NRCS, 2012). All landscape-scale and watershed-scale filters were summarized for the watershed area upstream of each reach.

We sampled stream physical characteristics (filters) and riparian vegetation during base flow conditions that coincided with the active growing season (June–September; Kershner *et al.*, 2004). Reach-level physical habitat metrics evaluated included stream gradient, bankfull width, bank stability, channel sinuosity, bank angle, median particle size, wood frequency, wetted width–depth ratio, residual pool depth, hydraulic radius and percent undercut banks (Table 2, Supporting Information Table S1; PIBO EM, 2012a). Vegetation data were collected along 42–50 greenline quadrats ($50\text{ cm} \times 20\text{ cm}$) per reach, on the basis of reach length and stream width. The greenline is the point at which the first rooted perennial vegetation adjacent to the stream is present (Winward, 2000; PIBO EM, 2012b) and usually occurs on the first flat, floodplain-like or depositional feature located at or near bankfull height. Vascular plant cover was measured for all species with at least 5% cover in the lower vegetation layer ($<1\text{ m}$ in height). Cover was also estimated within an upper woody species layer ($>1\text{ m}$). Cover was

estimated in seven classes: $\geq 5\text{--}15\%$, $\geq 15\text{--}25\%$, $\geq 25\text{--}38\%$, $\geq 38\text{--}50\%$, $\geq 50\text{--}75\%$, $\geq 75\text{--}95\%$ and $\geq 95\text{--}100\%$. Non-vegetation cover categories for wood, rock and bare ground were estimated in lower layer quadrats when vegetation was absent. Cover class midpoints were retained as the relative abundance for each species within each quadrat.

Data analysis

Vegetation data were analysed using a matrix of species relative cover within the lower and upper vegetation layers as determined for each reach. The stream reach was the experimental unit for all analyses. Plants not identified to the species level or not occurring in at least 5% of reaches were removed. The final vegetation dataset consisted of 112 lower and 29 upper layer species and seven ground-cover types at 720 reaches. This matrix was log + 1 transformed to compress large values, modulate small values and retain zero values in the dataset. Non-metric multidimensional scaling (NMDS) was implemented on a Bray–Curtis dissimilarity matrix of the transformed vegetation data to identify patterns in vegetation composition. On the basis of scree plots of ordination stress against the number of ordination axes, a three-dimensional NMDS solution was selected. To examine relationships between environmental filters and vegetation composition, environmental vectors were projected into the NMDS ordination solution and their significance tested using permutation tests (1000 Monte Carlo simulations). Partial redundancy analysis (pRDA) was used to partition the variance explained in the vegetation data by sets of landscape-scale, watershed-scale and reach-scale environmental filters (Liu, 1997). Year and management were treated as nominal variables within NMDS and pRDA. Environmental filter matrices were log + 1 transformed prior to pRDA analyses because of the log-normal structure of most environmental variables.

We identified vegetation communities on the basis of reach species composition using hierarchical agglomerative clustering (flexible beta method; $\alpha_1 = 0.625$, $\alpha_2 = 0.625$, $\beta = -0.25$). To identify which species were representative of identified vegetation clusters, we calculated indicator values for each species within each cluster using indicator species analysis (Dufrêne and Legendre, 1997). Indicator values are calculated as follows: $100 \times \text{relative abundance} \times \text{relative frequency}$ for each species within a cluster. A perfect indicator species receives an indicator value of 100. A species that is absent from a given cluster receives a value of zero. Indicator species significance was assessed with permutation tests (1000 permutations). We identified differences in environmental filters between vegetation communities using PERMANOVA (Anderson, 2001; Euclidean distance; 10 000 permutations) and the Tukey contrasts. To account for stream size effects on stream attributes, we included

bankfull width and gradient as covariates within models for all environmental filters. All analyses were performed using R 2.14.1 including the *vegan*, *cluster* and *labdsv* packages (Maechler *et al.*, 2002; R Development Core Team, 2011; Roberts, 2012; Oksanen *et al.*, 2013).

RESULTS

Do stream ecosystems of the interior Columbia River and upper Missouri River basins have distinct riparian plant communities?

We identified 10 distinct vegetation communities from cluster and indicator species analyses (cluster coefficient = 0.867; cophenetic correlation = 0.450; Bray–Curtis dissimilarity threshold = 1.70; Figures 3 and 4; Table 1 and Supporting Information Table S4). Forested communities occurred at high elevations with moderate to high mean annual precipitation and moderately steep gradients (Tables 1 and 2). A lodgepole pine–water sedge–Drummond’s willow community occurred at high elevation, moderately grazed, cool and wet reaches. This community’s strongest indicator species were *Salix drummondiana* and *Pinus contorta*. Within high-elevation, forested watersheds, a spruce–subalpine fir–heath–huckleberry community was common. *Picea engelmannii*, *Abies lasiocarpa* and *Vaccinium membranaceum*, species that tolerate heavy snowfall and cold climates, were the strongest indicators of this community. Within heavily forested, low elevation watersheds, a western redcedar–woodland fern–forb community occurred. Indicator tree species included *Thuja plicata* and *Abies grandis*, whereas the shade-tolerant ferns *Gymnocarpium dryopteris* and *Athyrium filix-femina* and forbs *Tiarella trifoliata* and *Circaea alpina* were strong understory indicators. A ponderosa pine–black cottonwood community occurred with *Pinus ponderosa* and *Populus balsamifera* as indicator tree species and hydrophytic graminoids *Scirpus microcarpus* and *Eleocharis palustris* as understory indicators. These species are tolerant of frequent low-intensity disturbance—fire for *P. ponderosa* and overbank flooding that scours mineral substrate to recruit *P. balsamifera*. Shallow water tables indicative of wetland soils corresponded to flood-tolerant *S. microcarpus* and *E. palustris*.

The highest elevation shrub cluster was a hydrophytic willow–scrub–shrub community. *Ribes hudsonianum*, *S. drummondiana*, *Lonicera invulcrata* and *Alnus incana* were woody indicator species, whereas *Chamerion angustifolium* was the strongest indicator species. This community occurred at higher gradient reaches. This community experienced severe fire disturbance in the decade prior to sampling, and burned *P. contorta* stands absent of overstory trees were common. A mock orange–snowberry–hawthorn–maple community consisting of *Philadelphus lewisii*, *Symphoricarpos albus*, *Acer glabrum* and *Crataegus douglasii* occurred at

Figure 3. Non-metric multidimensional scaling (NMDS) ordination of vegetation data plotted as individual reaches by identified vegetation communities (A). Environmental filters are plotted as vectors over community cluster centroids at the landscape (B), watershed-buffer (C) and stream (D) scales. Plotted vectors correspond to the strength of significant correlations ($p < 0.05$) between the final ordination solution and the variables within Table 2 and Supporting Information Tables S1 and S3. Black hulls within centroids are standard error of the mean.

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warm, low elevation, moderate gradient reaches within forested watersheds. A mesic woodland forb–shrub community occurred within heavily forested watersheds with indicator species: *Streptopus amplexifolius*, *Ribes lacustre*, *Cornus canadensis* and *Linnaea borealis*. A green alder–Sitka willow–mesic shrub–forb community (indicators: *Alnus viridis*, *Boykinia major*, *Ligusticum canbyi*, *Rubus parviflorus* and *Salix sitchensis*) occurred at larger channel reaches within high-elevation, forested watersheds (Table 2). This cluster also exhibited the largest median substrate size of all communities.

A Geyer's willow–Booth's willow–mesic meadow community occurred at grazed, dry, high-elevation stream reaches. *Salix geyeriana*, *Salix boothii* and graminoids *Juncus balticus*, *Poa pratensis* and *Carex nebrascensis* were indicator species. Highly sinuous, lower-gradient reaches with low water table depths and few undercut banks were characteristic of this community. A shining willow–Canada thistle meadow community was common at hotter, grazed

reaches. This community was composed of *Salix lucida* and *Cirsium arvense* and partially denuded of vegetation. Grazing allotments were very common within the riparian buffer and watershed. Both the Geyer's willow–Booth's willow meadow and shining willow–thistle meadow had low hydraulic radii, median substrate sizes and low residual pool depths.

Do environmental filters differ between vegetation communities?

Each landscape-scale environmental filter—watershed average, maximum and minimum elevation, average temperature and precipitation and annual precipitation—differed between at least two vegetation communities (Table 2). Watershed management filters—roads, forest cover and grazing—differentiated communities with similar landscape settings. Buffer and watershed slope and depth to the seasonal high water table also differentiated clusters of similar

Figure 4. Ten riparian vegetation communities were identified within the interior Columbia and upper Missouri River basins through cluster and indicator species analyses. Letters correspond to identified community types: lodgepole pine–water sedge–mesic shrub forest (A); denuded, willow–thistle (B); spruce, subalpine fir–heath–huckleberry forest (C); mock orange–snowberry–hawthorn–Douglas maple (D); mesic woodland forb–woody debris–prickly currant (E); western redcedar–woodland fern–grand fir forest (F); green alder–rock–Sitka willow–mesic shrub–forb (G); hydrophytic willow–scrub–shrub–horsetail (H); ponderosa pine–black cottonwood–mesic graminoid (I); Geyer’s willow–Booth’s willow–mesic rangeland graminoid–forb (J). This figure is available in colour online at wileyonlinelibrary.com/journal/rra

Table I. Indicator species for each riparian vegetation community derived by indicator species and cluster analyses

Community	Indicator species	Indicator value	Mean cover by plant community									
			A	B	C	D	E	F	G	H	I	J
(A) Lodgepole pine–water sedge–mesic shrub forest (n = 97)	<i>Salix drummondiana</i> (L)	29.66***	33.02	2.65	8.72	2.27	1.19	0	3.67	29.67	3.80	3.37
	<i>Pinus contorta</i> (U)	29.13***	27.49	9.96	7.24	1.77	0.42	0	3.22	0.30	5.72	1.28
	<i>Pinus contorta</i> (L)	19.53***	9.29	1.60	2.79	0	0.26	0	1.22	0	0.39	0.63
	<i>Carex aquatilis</i>	13.75***	13.71	5.69	4.05	3.93	1.74	0	2.51	0.30	2.74	9.55
	<i>Calamagrostis canadensis</i>	13.44***	11.41	3.95	6.92	2.20	2.69	0	5.06	10.79	1.81	4.25
(B) Denuded, willow–thistle (n = 94)	Bare ground (L)	12.03**	26.42	32.79	26.12	26.24	24.82	27.76	23.61	26.30	27.86	30.72
	<i>Salix lucida</i> (U)	10.46**	6.16	12.30	0	1.13	0	0	0.45	4.82	3.01	0.90
	<i>Salix lucida</i> (L)	8.35*	5.19	9.67	0	1.17	0	0	0.67	5.52	4.34	0.54
	<i>Cirsium arvense</i>	7.04*	1.36	3.79	0.63	1.92	0.53	0	0.16	0.91	1.88	2.00
(C) Spruce, subalpine fir–heath–huckleberry forest (n = 99)	<i>Picea engelmannii</i> (L)	27.05***	10.40	5.67	31.42	2.89	23.29	0	10.14	8.73	0.96	1.56
	<i>Picea engelmannii</i> (U)	26.9***	18.60	12.41	52.92	14.13	41.92	4.72	26.1	15.27	1.65	3.04
	<i>Abies lasiocarpa</i> (U)	24.57***	3.54	5.74	29.33	6.01	11.49	0	10.62	3.91	2.99	1.12
	<i>Abies lasiocarpa</i> (L)	20.30***	1.66	3.03	15.56	1.12	4.48	0	4.95	5.53	2.53	1.39
	<i>Vaccinium membranaceum</i> (L)	15.71***	0.31	0.67	9.72	0.61	2.89	1.66	7.26	0	0	0
	<i>Philadelphus lewisii</i> (L)	30.24***	0	1.72	0.20	13.18	0	0	0	0.61	0	0
(D) Mock orange–snowberry–hawthorn–Douglas maple (n = 136)	<i>Philadelphus lewisii</i> (U)	23.07***	0	1.54	0	13.53	0	0	0.32	2.20	0.96	0
	<i>Symphoricarpos albus</i> (L)	21.20***	1.51	9.38	2.00	26.36	15.82	15.68	11.93	4.46	17.88	0.13
	<i>Symphoricarpos albus</i> (U)	18.23***	0	3.09	0.30	14.27	6.18	3.16	8.02	0	5.87	0.54
	<i>Acer glabrum</i> (U)	13.00***	0.10	1.39	1.31	18.61	16.47	13.06	13.23	8.14	0.33	0
	<i>Streptopus amplexifolius</i>	25.51***	1.08	1.98	8.68	8.05	19.62	11.49	10.46	5.66	0	0.79
	<i>Ribes lacustre</i> (L)	16.51***	5.60	5.09	14.81	7.50	18.29	5.42	10.27	14.45	2.46	0.64
(E) Mesic woodland forb–woody debris–prickly currant (n = 76)	<i>Cornus canadensis</i> (L)	15.60***	0	0.11	1.09	1.53	6.02	1.62	1.27	2.58	0	0
	<i>Linnaea borealis</i> (L)	14.00**	0	1.61	1.96	2.01	7.19	5.38	4.24	0.61	0	0
	<i>Maianthemum stellatum</i>	11.09*	4.03	8.42	4.91	8.52	10.08	9.71	6.02	3.38	3.50	8.38
	<i>Thuja plicata</i> (L)	76.67***	0	0.45	0.90	2.62	7.06	48.78	3.82	0	0	0
	<i>Gymnocarpium dryopteris</i>	31.43***	0	0	1.79	2.87	11.40	17.02	3.97	0	0	0
	<i>Athyrium filix-femina</i>	30.30***	0.19	7.62	6.13	15.60	26.07	36.67	26.33	1.99	0.44	0
(F) Western redcedar–woodland fern–grand fir forest (n = 19)	<i>Tiarella trifoliata</i>	25.66***	0	0.67	1.31	1.11	5.01	9.38	1.79	1.89	0	0
	<i>Circaea alpina</i>	23.48***	0	1.73	1.04	2.92	4.25	9.09	1.97	0.61	0.63	0.17
	<i>Alnus viridis</i> (U)	36.25***	2.71	0.36	14.09	1.16	1.86	0	27.24	0.61	0.45	0
	<i>Boykinia major</i> (L)	31.92***	0.79	0.21	5.90	2.08	4.76	1.60	21.87	0	2.58	0
	<i>Alnus viridis</i> (L)	27.07***	3.15	0	14.07	1.10	1.11	0	19.10	2.67	0	0.91
	<i>Ligusticum canbyi</i>	17.38***	0.60	0.63	4.92	1.39	2.63	6.49	11.46	0.61	0	0
(G) Green alder–rock–Sitka willow–mesic shrub–forb (n = 62)	<i>Rubus parviflorus</i> (U)	16.31***	0	0	0	11.96	7.94	0	13.79	1.76	0	0
	<i>Chamerion angustifolium</i>	33.47***	7.65	5.21	3.93	4.47	1.55	0.53	3.83	20.91	2.30	2.62
	<i>Ribes hudsonianum</i> (L)	32.50***	12.82	17.87	16.22	10.97	21.06	1.87	9.17	47.89	3.74	1.30
	<i>Salix drummondiana</i> (L)	28.40***	33.02	2.65	8.72	2.27	1.19	0	3.67	29.67	3.80	3.37
	<i>Ribes hudsonianum</i> (U)	26.86***	0.96	3.18	1.85	3.42	7.10	0	2.18	18.96	0.86	0
	<i>Lonicera involucrata</i> (L)	25.78***	11.93	1.75	10.20	4.59	17.61	1.05	16.41	31.51	1.26	0

(Continues)

Table I. (Continued)

Community	Indicator species	Indicator value	Mean cover by plant community									
			A	B	C	D	E	F	G	H	I	J
(I) Ponderosa pine–black cottonwood–mesic graminoid (n=46)	<i>Pinus ponderosa</i> (U)	19.37***	0.33	3.71	0.63	6.54	1.09	3.29	0.32	7.54	21.01	0.35
	<i>Scirpus microcarpus</i>	16.57***	2.99	7.51	0.27	4.52	1.66	2.11	4.69	0	14.73	0.17
	<i>Eleocharis palustris</i>	15.12***	0.88	0.52	0	0.12	0	0	0	0	4.67	2.54
	<i>Phleum pratense</i>	10.60**	2.94	2.80	0.56	2.22	0	0	0	0.76	6.29	3.79
	<i>Mentha arvensis</i>	9.20**	1.64	4.04	0.74	4.42	1.36	0.79	0.85	4.46	7.27	1.93
(J) Geyer's willow–Booth's willow–mesic rangeland graminoid–forb (n=58)	<i>Juncus balticus</i>	33.16***	3.87	3.90	0.51	1.40	0.26	0	0.16	0	8.61	15.13
	<i>Salix geyeriana</i> (L)	22.58***	2.25	3.76	0.92	0	0	0	3.21	0.62	1.62	14.12
	<i>Salix geyeriana</i> (U)	22.05***	3.71	5.47	0	0	0	0	1.37	0.46	1.41	16.42
	<i>Poa pratensis</i>	20.28***	4.64	10.37	0.73	3.95	0.80	0.13	0.67	5.34	9.10	12.28
	<i>Salix boothii</i> (U)	18.69***	19.55	8.99	3.83	0.97	0.67	0	1.39	21.09	1.98	27.37

Up to five statistically significant species per cluster are presented. Woody species that can occur in either vegetation layer are denoted by (L) for the lower vegetation layer and by (U) for the upper vegetation layer. Non-vegetation ground cover classes are in bold text. Indicator species statistical significance was calculated using 1000 permutations and are indicated by asterisks: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Full community indicator species lists are presented in Supporting Information Table S4.

landscape settings (Table 2). The fluvial habitats at which each vegetation community occurred differed based on numerous stream filters (Table 2). Gradient, hydraulic radius, bankfull width and wetted width–depth ratio, attributes of channel form and size, differed between most vegetation communities. Bank stability and residual pool depth did not differ between any communities, whereas sinuosity was only significantly higher in the Geyer's willow–Booth's willow–meadow community than other communities. Instream wood and particle size, attributes that respond to both channel form and stream size, differed between communities. The fit of environmental filters to the final NMDS solution (stress = 19.92; $p < 0.01$; $R^2 = 0.96$ non-metric fit) shows the directional relationships between statistically significant environmental filters and individual community clusters within the ordination (Figure 3; Supporting Information Table S2).

At what spatial scales are environmental filters most responsible for shaping riparian vegetation assemblages?

Variance partitioning showed that landscape level filters explained the greatest variability within the vegetation data (26.2%; Figure 5; Supporting Information Table S3). The joint effects of landscape and watershed filters (19.7%), stream filters (15.3%), joint effects of landscape, watershed and stream filters (15.0%) and watershed filters (13.2%) explained much of the remaining variance in the vegetation data. Landscape-stream filter and buffer-stream filter joint effects corresponded to only 7.2% and 3.4% of the explained variance within vegetation data. Environmental filters from all scales were correlated to the final NMDS solution. Model fit between landscape-scale filters and the NMDS solution were the best of the three filter scales (Figure 3), with minimum and average elevation, average temperature, latitude, maximum elevation and average precipitation being most strongly correlated to vegetation composition. Watershed filters showed that grazing in the buffer and watershed, proportions of the buffer and watershed that were forested, and buffer slope were also strongly correlated to vegetation. The stream filters that fit best to the NMDS solution were bank angle, undercut banks, wood frequency, hydraulic radius and sinuosity.

DISCUSSION

Environmental filters and vegetation community assembly

Within the interior Columbia and upper Missouri River basins, distinct riparian plant communities assembled in response to landscape-scale, watershed-scale and stream-scale environmental filters. Landscape-scale filters explained the most variability in vegetation composition. Across the

Table II. Mean values for each environmental filter at the stream, buffer and landscape scales for each identified vegetation community cluster

Scale	Variable	Community cluster									
		A	B	C	D	E	F	G	H	I	J
Landscape	30-year average precipitation (m)	0.89 ^{ad}	0.78 ^{ab}	1.11 ^c	0.91 ^d	0.91 ^d	1.29 ^{ce}	1.32 ^e	0.93 ^{ad}	0.72 ^b	0.69 ^b
	30-year average temperature (°)	2.2 ^b	4.3 ^a	2.4 ^b	5.0 ^c	4.1 ^{ad}	5.0 ^{ac}	4.0 ^b	3.1 ^{ad}	4.9 ^a	2.9 ^d
	Annual precipitation (m)	0.84 ^{bc}	0.77 ^{ab}	1.08 ^c	0.89 ^b	0.89 ^b	1.29 ^{cd}	1.29 ^d	0.84 ^{ab}	0.71 ^{ac}	0.69 ^a
	Latitude (°)	44.94 ^a	45.18 ^a	46.25 ^b	46.61 ^b	47.45 ^c	47.85 ^c	46.66 ^b	44.65 ^{ad}	45.05 ^a	43.88 ^d
	Longitude (°)	-114.36 ^{ce}	-115.51 ^{ab}	-114.67 ^{ac}	-116.14 ^b	-115.68 ^b	-116.13 ^{abd}	-115.34 ^{abe}	-115.12 ^{abe}	-117.34 ^d	-113.69 ^c
	Average elevation (m)	2290.0 ^{ef}	1841.3 ^a	2068.6 ^b	1501.7 ^{cd}	1533.0 ^{cd}	1312.7 ^c	1662.1 ^{ad}	2079.3 ^{bc}	1675.7 ^{ad}	2337.0 ^f
	Minimum elevation (m)	1909.9 ^g	1446.0 ^{ab}	1713.1 ^c	1038.0 ^{de}	1168.1 ^{ef}	862.4 ^d	1161.6 ^{ef}	1526.6 ^{ac}	1304.5 ^{bf}	1962.4 ^g
	Maximum elevation (m)	2782.5 ^e	2347.9 ^{ab}	2507.4 ^{ac}	1979.1 ^d	1971.2 ^d	1837.5 ^d	2189.6 ^{bd}	2649.0 ^{ce}	2208.8 ^{bd}	2848.1 ^e
	Igneous rock (%)	54.52	56.72 ^{ab}	51.09 ^{bc}	47.50 ^{bc}	35.04 ^{cd}	12.04 ^d	37.36 ^{acd}	86.72 ^e	65.68 ^{bc}	35.18 ^{acd}
	Metamorphic rock (%)	21.35 ^{ab}	24.20 ^{ab}	31.91 ^{bc}	33.72 ^{ac}	46.58 ^{cd}	69.04 ^d	48.33 ^{cd}	9.02 ^b	11.64 ^b	14.54 ^b
	Sedimentary rock (%)	18.46 ^a	10.70 ^a	11.13 ^a	13.99 ^a	9.48 ^a	13.05 ^a	11.57 ^a	2.40 ^a	17.80 ^a	41.63 ^b
	Unconsolidated rock (%)	5.57 ^a	8.30 ^a	5.72 ^a	4.76 ^a	8.82 ^a	5.75 ^a	2.61 ^a	1.82 ^a	4.87 ^a	8.64 ^a
	Stream density (km/km ²)	1.25 ^{ab}	1.32 ^a	1.11 ^b	1.54 ^c	1.20 ^{ab}	1.33 ^{abc}	1.39 ^{ac}	1.42 ^{ac}	1.41 ^{ac}	1.39 ^{ac}
	Roads in buffer (%)	0.79 ^b	1.73 ^a	0.88 ^b	1.75 ^a	1.68 ^a	1.24 ^{ab}	0.68 ^b	0.61 ^b	2.64 ^c	1.10 ^{ab}
Watershed	Forested in buffer (%)	66.52 ^{ad}	59.87 ^a	80.37 ^b	73.81 ^c	76.54 ^{bc}	73.86 ^{bcd}	81.36 ^b	63.31 ^{ad}	68.70 ^{cd}	47.09 ^e
	Grazing in buffer (%)	57.23 ^{aef}	73.22 ^{ab}	31.70 ^{cd}	48.73 ^{de}	37.60 ^{df}	21.01 ^{cd}	11.05 ^c	44.44 ^{de}	64.59 ^{be}	85.58 ^b
	Average buffer slope (%)	30.26 ^{bc}	33.64 ^{ab}	28.54 ^c	38.42 ^d	33.25 ^{ac}	40.74 ^{ad}	38.40 ^{ad}	44.19 ^d	29.43 ^{bc}	31.48 ^{bc}
	Roads in watershed (%)	0.57 ^b	1.41 ^a	0.67 ^b	1.45 ^a	1.43 ^a	1.19 ^{ab}	0.69 ^b	0.44 ^b	1.85 ^a	0.64 ^b
	Forested in watershed (%)	69.93 ^a	68.92 ^a	79.77 ^b	82.32 ^b	87.50 ^b	85.17 ^b	85.52 ^b	66.74 ^a	79.60 ^b	47.20 ^c
	Grazing in watershed (%)	57.12 ^{aef}	72.78 ^{ab}	31.09 ^{cd}	48.50 ^{de}	36.81 ^{df}	20.69 ^{cd}	10.57 ^c	44.45 ^{de}	63.60 ^{be}	85.24 ^b
	Average watershed slope (%)	35.98 ^{bc}	33.81 ^{ab}	37.71 ^{bc}	37.82 ^{bc}	35.15 ^{ac}	43.36 ^{cd}	41.01 ^{cd}	46.98 ^d	29.29 ^a	34.88 ^{ac}
	Erosivity (unitless, higher values = less erosive)	132.35 ^a	140.48 ^{ab}	168.71 ^b	159.52 ^{ab}	149.74 ^{ab}	148.74 ^{abc}	159.16 ^{ab}	175.09 ^{ab}	141.94 ^{ab}	83.16 ^c
	Watershed area (km ²)	40.56 ^a	33.50 ^a	25.56 ^a	45.32 ^a	25.13 ^a	27.32 ^a	59.12 ^a	45.65 ^a	156.98 ^b	40.11 ^a
	Average soil thickness (m)	1.78 ^{ab}	1.76 ^{ab}	1.75 ^{ac}	1.80 ^b	1.80 ^b	1.80 ^{ab}	1.73 ^a	1.79 ^{ab}	1.81 ^b	1.80 ^{bc}
	Average depth to water table (m)	1.07 ^b	1.15 ^{abc}	1.12 ^{bc}	1.22 ^{cd}	1.30 ^d	1.34 ^{ad}	1.22 ^{cd}	0.88 ^e	1.09 ^{bc}	1.11 ^{bc}
	Watershed burned (%)	18.73 ^{ac}	9.71 ^{ab}	6.74 ^b	11.03 ^{ab}	7.03 ^{ab}	0.42 ^{ab}	4.31 ^b	32.07 ^c	9.85 ^{ab}	2.7 ^b
	Management	79	90	66	119	66	15	44	20	44	56
	Managed Reference	18	4	33	17	10	4	18	13	2	2

(Continues)

Table II. (Continued)

Scale	Variable	Community cluster									
		A	B	C	D	E	F	G	H	I	J
Stream	Bank stability (%)	95.74 ^a	95.72 ^a	95.90 ^a	96.27 ^a	97.42 ^a	96.50 ^a	98.15 ^a	98.48 ^a	96.16 ^a	96.27 ^a
	Gradient (%)	1.44 ^b	1.86 ^{ab}	1.63 ^b	2.26 ^{cd}	2.46 ^{cd}	2.53 ^{cd}	2.17 ^d	2.65 ^d	1.69 ^{bc}	1.68 ^b
	Sinuosity (ratio)	1.33 ^a	1.26 ^a	1.34 ^a	1.18 ^a	1.21 ^a	1.14 ^a	1.13 ^a	1.21 ^a	1.23 ^a	1.58 ^b
	Bankfull width (m)	6.76 ^{bc}	5.67 ^{ab}	6.81 ^{bc}	6.54 ^{bc}	5.01 ^{ab}	8.06 ^{cd}	10.97 ^d	6.14 ^{bc}	7.22 ^{bc}	4.61 ^a
	Hydraulic radius (m)	0.45 ^{bc}	0.38 ^{ab}	0.47 ^c	0.41 ^{bc}	0.37 ^{ac}	0.41 ^{ac}	0.52 ^{bc}	0.41 ^{bc}	0.36 ^a	0.36 ^{ab}
	Bank angle (°)	106.23 ^{ad}	110.86 ^{ab}	96.55 ^c	116.41 ^b	98.09 ^{cd}	111.37 ^{abc}	110.13 ^{ac}	115 ^{ab}	128.65 ^e	116.09 ^{be}
	Median substrate size (m)	0.05 ^{ab}	0.03 ^a	0.04 ^{ab}	0.06 ^b	0.04 ^{ab}	0.07 ^a	0.11 ^c	0.06 ^{ab}	0.05 ^{ab}	0.03 ^a
	Wood frequency (pieces/km)	205.02 ^b	219.43 ^{ab}	471.82 ^c	243.72 ^{ab}	425.93 ^c	451.81 ^{ac}	258.40 ^{bd}	184.34 ^{ab}	135.15 ^{bd}	31.01 ^d
	Wetted width–depth ratio	24.60 ^a	22.09 ^a	25.01 ^a	28.04 ^a	21.63 ^a	28.17 ^a	35.58 ^a	24.04 ^a	29.66 ^a	17.51 ^a
	Residual pool depth (m)	0.38 ^a	0.31 ^a	0.38 ^a	0.33 ^a	0.27 ^a	0.38 ^a	0.43 ^a	0.30 ^a	0.39 ^a	0.30 ^a
	Undercut banks (%)	36.21 ^{ad}	32.34 ^{ab}	44.85 ^c	26.36 ^b	43.34 ^{cd}	31.18 ^{abc}	31.62 ^{ad}	26.93 ^{abc}	18.21 ^e	26.64 ^{bc}

Lowercase letters indicate group membership based on the Tukey honest significant difference pairwise comparisons for differences in each filter for each vegetation community cluster membership. Bankfull width and gradient were used as covariates in these tests.

interior Pacific Northwest, biophysical and climatic gradients synergistically shape vegetation alongside fine-scale biotic and abiotic environmental filters (Sarr and Hibbs, 2006). The timing and intensity of watershed-scale disturbances such as grazing and fire, and channel form characteristics (e.g. bankfull width and gradient) often correspond to regional climate (Miles *et al.*, 2000). Vegetation communities with similar climate or landscape settings often differed in their watershed-scale and/or stream-scale filters. For example, the tree-depauperate, mesic woodland forb and *A. grandis* and *T. plicata*-dominated western redcedar communities occurred in similar landscape-scale and stream-scale environmental settings (Table 2), but watershed management activity differed greatly. The mesic woodland forb community's watersheds had higher road densities and were more frequently grazed than the western redcedar community (Table 2). This example suggests that when higher-order filters are held constant, disturbance thresholds may shape riparian vegetation communities (Sarr *et al.*, 2011).

Multi-scale environmental filters have been shown to drive many watershed attributes, including stream habitat variability (Roper *et al.*, 2007), fish community assembly (Tonn, 1990), water quality (Varanka and Luoto, 2012) and benthic invertebrate community structure (LeCraw and Mackereth, 2010). Accordingly, it is not surprising that multiple environmental filters also shape forest (Díaz *et al.*, 1998), riparian (Sarr and Hibbs, 2006, 2007) and wetland (Hough-Snee *et al.*, 2011, 2013) vegetation communities in addition to local hydrology and geomorphology. Chambers *et al.* (2004) demonstrated that Great Basin riparian vegetation communities correspond to distinct stream geomorphic attributes: terrace abundance and height, bankfull width–depth ratio, bankfull and incised channel depths, median particle size and fine sediment. Our work integrates these studies into a conceptual model of how riparian vegetation assembles in response to multiple environmental gradients at sub-continental scales. Plant species pools first pass through climatic and geologic (landscape) filters before being filtered down by watershed-scale physical attributes and instream hydrogeomorphic (stream) filters to arrive at a given reach (Figure 1). The resulting vegetation community interacts with local hydrology, physical structures (e.g. large wood) and hydraulics to engineer channel and streambank forms that shape plant microhabitats.

While we measured landscape-scale, watershed-scale and stream-scale filters, finer-scale environmental filters may also shape riparian plant community assembly. Competition (Van Pelt *et al.*, 2006), insolation heterogeneity (Sarr and Hibbs, 2007), intra-annual variation in soil moisture (Stolnack and Naiman, 2010) and disturbance (Swanson *et al.*, 1998) also affect riparian vegetation. Both Whigham *et al.* (2012) and Goebel *et al.* (2012) found that fine-scale biotic (competition) and abiotic (overbank flooding) environmental drivers

are responsible for riparian community assembly within head-water streams. Differences in the interpretation of whether large-scale or fine-scale environmental filters drive riparian vegetation may be attributable to differences in study extent (McGill, 2010). Because most consequential land management decisions (grazing, road management, timber harvest, etc.) take place at the scale of hundreds to thousands of hectares, large-scale processes are often emphasized in landscape planning. However, we show here that filters from many scales shape vegetation across landscapes. We classified riparian vegetation across two large, targeted watersheds, but within smaller catchments, landscape-scale or watershed-scale filters alone may not provide sufficient insight to effectively inform land use planning. Watershed-scale, stream-scale and finer-scale filters should all be considered when assessing environmental drivers of vegetation in small basins.

Stream-scale filters and channel form: vegetation as a response and driver

Tight connections between fluvial, riparian and terrestrial environments are well documented in small-sized to mid-sized streams such as those studied here (Vannote *et al.*, 1980). Stream attributes corresponded to distinct riparian plant communities, and this vegetation has the potential to further modify stream geomorphic character (Corenblit *et al.*, 2007). Vegetation feedback that modifies the fluvial environment may exert filtering effects on what species can colonize and persist at a given location. Decoupling which stream-scale environmental filters *drive* vegetation and which habitat attributes *respond* to vegetation requires careful interpretation of how vegetation and stream morphology interact (Bendix and Stella, 2013). Our finding that

Figure 5. Venn diagram of pRDA variance partitioning for the constrained proportion of the inertia (22.4%) using environmental filters at the stream, watershed-buffer and landscape scales. The individual filters within each variable set are summarized in Supporting Information Tables S1 and 2. Full pRDA results are presented in Supporting Information Table S3

distinct vegetation communities corresponded to distinct channel form complements studies that have shown allochthonous riparian subsidies to streams—nutrients, habitat-forming wood and terrestrial invertebrates—all vary on the basis of riparian ecosystem structure (DeLong and Brusven, 1994; Richardson and Danehy, 2007; Hough-Snee *et al.*, 2014). Accordingly, riparian vegetation serves as a filter on stream physical habitats and their associated aquatic biota (Poff, 1997).

The stream physical settings within which riparian plant communities occur provide insight into the environmental filters that riparian vegetation has recently responded to. For example, montane conifer forests occurred in low-gradient channels with efficient hydraulic radii, moderate to high sinuosity and frequent undercut banks. Within forested communities, mechanical disturbance from recent overbank floods may not be intense enough to push vegetation communities away from large trees and toward disturbance tolerant shrubs and graminoids. Shrub–forb systems had higher gradients than forests, indicating that they may experience higher stream power that physically disturbs vegetation, selecting for woody species that resprout following disturbance (Table 2). Forest vegetation feeds back on stream-scale filters both directly and indirectly. Trees stabilize stream banks with large root networks and are more likely to introduce wood to the channel than herbaceous community types (direct effects; e.g. Hough-Snee *et al.*, 2014). Instream wood, a product of vegetation and landscape setting, may be evacuated from reaches with high stream power, whereas in lower-gradient systems, wood may slow streamflow, form pools, raise water tables and create wetland meadows incapable of supporting trees (indirect effects).

Streambed particle size also interacts with vegetation and can be reduced by watershed disturbances such as logging or grazing that introduce fine sediment (Kasprak *et al.*, 2013). Plant propagules, such as those of the pioneer species in the green alder–Sitka willow or burned lodgepole pine communities, may germinate and persist in deposited fine sediment. Once established, these shrubs can create hydraulic diversity along stream banks, sort sediment and encourage the formation of undercut banks. Shrub colonization can also cause channel narrowing (Dean and Schmidt, 2011), increasing relative stream power and bank friction that increase shear stress and alter sediment transport. These hydraulic feedback directly influences riparian landforms available for vegetation colonization.

Vegetation responses to rapidly changing filters during global change

Riparian vegetation may respond to filters that originate at small spatial scales more rapidly than gradually changing

landscape-scale filters (Sarr and Hibbs, 2007). The temporal scales at which stream channels, riparian landforms and vegetation adjust to shifting fine-scale hydrogeomorphic filters are quite rapid (Wolman and Gerson, 1978; Sarr and Hibbs, 2007). Within low-order streams of the Pacific Northwest, riparian vegetation is subject to the direct effects of flooding, deposition, erosion and physical disturbance associated with spring runoff floods. How landscape-scale filters influence vegetation may be less direct (e.g. temperature warming) than hydrogeomorphic or watershed filters (flooding, fire, etc.) that rapidly shape entire communities through disturbance. Broad global change—shifts in climate, land use and natural disturbance regimes—will likely cause changes in the timing and intensity of environmental filters. These changes in climate and watershed processes will interact with anthropogenic watershed management for uses such as grazing and timber extraction, rapidly shaping the trajectories of riparian vegetation communities and their associated stream habitats.

Although we see clear patterns between environmental filters and vegetation composition, how these filters interact with one another in the future will further shape riparian vegetation assembly. For example, changes in landscape filters such as precipitation and temperature will shift the intensity, duration and timing of peak stream discharge that stream channel form. These climatic shifts may reduce the frequency, duration and intensity of overbank flooding as well as hydrologic connectivity between streams and riparia. Novel hydrologic conditions in heretofore unregulated low-order streams may lead to declines in riparian plant communities that rely on seasonal floods for sediment deposition, propagule dispersal and seedling establishment or to reduction of terrestrial plant competition (Merritt *et al.*, 2010). Riparian plant community changes resulting from this shifting environmental baseline have the potential to further alter stream habitats. Because changes in riparian vegetation and stream physical form will be tied to multiple environmental filters, it is paramount that riparian vegetation, multi-scale environmental filters and stream physical habitat are concurrently assessed to disentangle which filters most strongly affect riparian vegetation and how vegetation feeds back on aquatic habitat change. By exploring how today's vegetation corresponds to recent environmental conditions, it may be possible to infer future stream trajectories as climate, watershed management, and disturbance regimes shift in an era of unprecedented global change.

ACKNOWLEDGEMENTS

We thank Eric Archer, Kern Ewing, Jim Gore, Lexine Long, Wally Macfarlane, Christy Meredith, Lloyd Nackley, Jeff Ojala, Mike Scott, Andrew Van Wagenen and two anonymous reviewers for project support and/or comments that

improved the manuscript and numerous USDA Forest Service employees for data collection and stewardship. This research is a contribution of the USDA Forest Service PACFISH/INFISH Biological Opinion Effectiveness Monitoring Program, supported by USDA Forest Service Regions 1, 4 and 6, and numerous Bureau of Land Management Field Offices. N.H.-S. was supported in part by a Utah State University Presidential Fellowship during manuscript drafting and revision.

STATEMENT OF AUTHOR CONTRIBUTIONS

N.H.-S. conceptualized the project, managed data and performed analyses. B.B.R. guided analytical workflows. N.H.-S. and R.R.L. created figures and tables. N.H.-S., B.B.R., J.M.W. and R.R.L. wrote the manuscript.

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