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The transition from riparian to upland forest plant communities on headwater streams in the southern Sierra Nevada, California, United States[1,2]

Christopher R. Dolanc[3]
Department of Biology, Mercyhurst University, 501 E. 38th Street, Erie, PA 16546

Carolyn T. Hunsaker
Pacific Southwest Research Station, Forest Service, US Department of Agriculture, 2081 E. Sierra Avenue, Fresno, CA 93710

Abstract. Fixed-width buffer zones on rivers and streams are designed to protect the diverse riparian community and its important function in the ecosystem. However, recent data suggest that riparian areas of some western forests have become more fire prone because of restrictions on fuel reduction treatments within buffer zones. Surprisingly little is known about where and how the plant community transitions from riparian to upland vegetation, but understanding that transition would inform the restoration of riparian forest structure and function and its associated management applications (*e.g.,* prescribed fire or mechanical thinning) that may be necessary to achieve restoration. Using data collected from the Kings River Experimental Watersheds, we assessed the transition in plant structure and composition from riparian near-stream areas to upland locations, in mixed-conifer and red fir forests on headwater streams of the southern Sierra Nevada, CA. Our data strongly support the conclusion that the riparian zone, as evidenced by the riparian plant community, extends beyond 10 m from the stream on these narrow, first- and second-order streams. The herbaceous community at 10 m from the stream was distinct from the upland community and had greater similarity to locations closer to the stream in mixed-conifer forest. Species richness was three to four times greater in riparian areas compared with upland areas, and there was little overlap of the more-abundant herbaceous species. In addition, riparian forests were generally denser, with smaller trees in mixed-conifer forest, but had similar stand structure to upland forests in red fir forest. Differences between mixed-conifer and red fir forests may reflect different departures from the historical fire regime in these two community types. Compared with riparian areas of wetter climates, riparian areas of dry climates, such as the Sierra Nevada, may harbor even greater species diversity relative to nearby upland areas, indicating that buffer zones of restricted management may be justified in these forests if the goal is the preservation of biodiversity. However, perhaps more important, these findings, along with recent literature, highlight the need to identify site-specific goals when undertaking restoration of riparian forests in the western USA: herbaceous biodiversity, fuels reduction, historic tree composition and structure, and/or water quality.

Key words: buffer zone, forest management, headwater streams, Kings River Experimental Watersheds (KREW), plant community, prescribed burning, riparian, Sierra Nevada, stream management zone, upland

Riparian areas are widely recognized for their role in wildlife habitat, stream protection, conservation of biodiversity, and critical hydrologic processes (Gregory *et al*. 1991, Naiman *et al*. 2001). By definition, the riparian area extends out from the stream to the limits of flooding (Gregory *et al*. 1991), but the stream's influence on the microclimate may extend well beyond that (Brosofske *et al*. 1997), at least for many types of riparian areas. Riparian plant species are often indigenous to the near-stream zone and are frequently considered rare and/or critical to the ecosystem. Riparian plant composition varies at fine, temporal and spatial scales along the length of the stream (Naiman *et al*. 1993) and is often distinct from upland composition (Sabo *et al*. 2005). Along many small streams, the transition from riparian to upland plants appears visually to occur very near the stream, but it is unclear

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[3] Author for correspondence: cdolanc@mercyhurst.edu

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whether actual differences in the plant community support that.

Because of their significant contribution to ecosystem services and health, riparian areas in North America have gained protection in the form of *buffer zones* to conserve water quality and protect both the aquatic and riparian ecosystems (Richardson *et al*. 2012). The literature is ambiguous on the use of the term, however; the term *buffer zone* is usually used when no activity is allowed, and the term *stream management zone* (or *streamside management zone*) is used by government agencies to indicate an area where restrictions can be placed on a diverse array of management activities, such as herbicide use, fuel storage, new road construction, prescribed burning, and tree harvesting. The reasons for restrictions on activities in near-stream areas can include one or more of the following: protection of water quality and aquatic organisms, maintenance of cooler water and air temperatures, reduction of stream sedimentation, and protection of riparian plant biodiversity and specialized species. In the western USA, the application of buffer zones and stream management zones is increasingly being called into question when the objective of management is the restoration of historic fire regimes and/or forest structure. Buffer zones tend to be a fixed-width, regardless of the size of the stream/river or history of the site (Richardson *et al*. 2012). Some riparian forests have structures similar to that of adjacent uplands, suggesting their fire regimes were historically similar (Dwire *et al*. 2015). Other forests show greater tree densities and fuel loads in the riparian forest than their upland counterparts have (Van de Water and North 2011, Messier *et al*. 2012), posing risks of high-severity fire and potentially propagating fire through the landscape of treated, upland areas with reduced fuel loads (Agee 1998). Historically, in arid western mountains, fire probably burned nearly as frequently in riparian areas as in upland areas for some forest types (Dwire and Kauffman 2003, Skinner 2003, Van de Water and North 2010), despite the fact that riparian areas often have moister microclimates. Stone *et al*. (2010) reported that fire managers were proceeding cautiously with fuel treatments in riparian areas on western US National Forests. More information is needed regarding riparian plant composition and width to assess various objectives, such as the protection of rare and sensitive riparian species and the restoration of forest structure and fire regimes.

In the Sierra Nevada of California, understanding how to manage riparian forests is of particular importance because most of the middle and high elevations ($>$ 1,000 m) are managed by federal land agencies (SNEP 1996), and most of the state of California depends heavily on runoff from streams on that land (Kattelman 1996). Buffer-zone width for perennial streams on national forest land in this region is typically 91 m on each side of the stream (USDA 2001). However, that width should probably be flexible, depending on many factors, such as stream size, site history, and management goals (Hunsaker and Long 2014). Fire suppression in mixed-conifer forests in the Sierra Nevada has been extensive, and much of the landscape has not had fire for 80–100 yr, despite a mean historical fire-return interval of 12 yr (North 2014). In addition, the arid Mediterranean climate of the Sierra Nevada means that differences between plant communities that grow in dry soils *vs*. those with access to water should be stronger than in climates with consistent growing-season moisture, which suggests that protecting their narrow riparian zones may be even more important than in more mesic regions.

In this article, we characterize the transition from riparian to upland forest plant communities on perennial headwater streams in conifer forests of the southern Sierra Nevada, CA. Our objectives were twofold: (a) determining the extent of the riparian plant community in those headwater streams to inform management practices, and (b) determining whether riparian buffer zones should be managed for fuel-load reduction, as in upland forest. We subdivided the riparian zone and analyzed the community at locations progressively farther from the stream edge and compared them to upland locations. The streams in our study area were narrow (generally $<$ 2 m wide) and often immediately gave way to steep hill slope regions. Data on microclimate from our study area indicated the influence of the stream was limited to within 7.5 m (Rambo and North 2008). Therefore, our hypotheses for this study were as follows: (a) the riparian plant community beyond 7.5 m from the stream are more similar to the upland plant community than to the riparian plant communities closer to the stream, and (b)

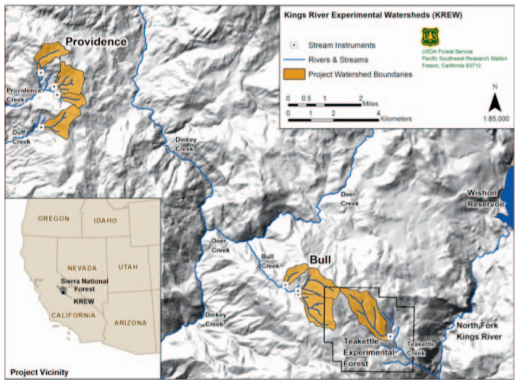

FIG. 1. Location of the study area within the Kings River Experimental Watersheds (KREW), Sierra National Forest, CA, showing the two clusters of four watersheds each in KREW: Providence Creek, and Bull Creek.

because of the similar fire histories of riparian and nearby upland regions, the riparian zones will have forest structures similar to the upland forest.

Materials and Methods. STUDY AREA. All sampling was carried out on watersheds within the Kings River Experimental Watersheds (KREW), located in the Sierra National Forest, southern Sierra Nevada, CA (Fig. 1). These watersheds exist in two clusters: (a) Providence Creek, which ranges from 1,524-m to 2,094-m elevation, and (b) Bull Creek, which ranges from 2,062-m to 2,498-m elevation; the two clusters were approximately 12 km apart (Fig. 1). The work reported here is a unique and important component of the larger KREW paired-watershed experiment, which is designed to inform future forest management. Vegetation of Providence Creek is broadly classified as a mixed-conifer forest, dominated by *Abies concolor* (Gordon & Glend.) Hildebr. (white fir), *Calocedrus decurrens* (Torr.) Florin (incense cedar), *Pinus lambertiana* Douglas (sugar pine), *Pinus ponderosa* var. *pacifica* J.R. Haller & Vivrette (Pacific ponderosa pine), and hardwoods, most commonly *Quercus kelloggii* Newb. (California black oak). Vegetation of Bull Creek is classified as an *Abies magnifica* A. Murray bis (California red fir) forest but is transitional from a mixed-conifer forest to a red fir forest at its lower elevations. *Abies magnifica* is singly dominant in most locations, with *A. concolor* secondarily dominant at lower elevations and drier slopes. Typical of the mixed-conifer forest *vs.* red fir forest, Providence Creek forests are generally more complex, with denser understory shrubs, more canopy species, and some very dense stands. For more information on the vegetation types discussed and their component species, see Potter (1998), Fites-Kaufman *et al.* (2007), and Sawyer *et al.* (2009).

Climate in both locations is montane Mediterranean, characterized by warm, dry summers and cool, wet winters with nearly all of the precipitation falling between October and May (Minnich 2007). The average (mean + SD) annual precipitation from 2005 to 2015 was 132 ± 32 cm yr^{-1} at the Bull Creek site and 127 ± 58 cm yr^{-1} at the Providence Creek site. From 2004 to 2007, the fraction of precipitation that fell as snow at the Bull Creek site was 75–90% compared with 35–60% at the Providence Creek site (Hunsaker *et al.* 2012). The precipitation in water year (October 1–September 30) 2005 was above average, with 182 cm at Bull Creek and 174 cm at Providence Creek. Soils of both sites were derived from granite or granodiorite and were in the Cagwin, Gerle-Cagwin, and Shaver series (Johnson *et al.* 2011). A detailed comparison of the soil physical and chemical characteristics for the two watershed clusters can be found in Johnson *et al.* (2011). More detail on climate and hydrology can be found in Hunsaker *et al.* (2012).

The riparian areas in our study site bordered the headwater, perennial streams (Fig. 2), which range in length from 596 m to 3,171 m (Table 1), and were first- and second-order streams with widths of 0.6–1.6 m and low width to depth ratios of 7.1–10.5. Most of the streams are slightly entrenched (incised; entrenchment ratio > 2.2), with two streams considered moderately entrenched (1.4–2.2), according to Rosgen (1994). For more information on KREW, its physical characteristics, and its instrumentation, see Hunsaker *et al.* (2012).

FIELD SAMPLING. Sampling for this study was performed in 2005 on 48 riparian and 108 upland plots (Table 1). A few plots that occurred entirely within meadows were sampled but not analyzed in this study because our emphasis was on forested communities. Riparian vegetation plot locations were chosen systematically based on the length of

(A)

(B)

FIG. 2. Photos of the stream in the P301 watershed, which occurs at an intermediate elevation within the study area and is an intermediate stream length and watershed area (Table 1). Photos show (A) main channel of P301 looking upstream in mid-summer form, and (B) the same stream channel, looking upstream in early spring, after snowmelt. Note the narrow "greenline" in both photos. As shown, an average human adult can easily step across the channel at most locations along the stream.

the stream, with the shortest stream receiving 5 plots and longest stream receiving 10 plots (Table 1). The first plot on each stream was 50 m upstream of the flume (see Hunsaker *et al*. 2012 for more information on stream instrumentation) and continued on alternating sides of the main stream channel. For upland areas, plot locations were chosen by stratified, random selection, based on a uniform sampling grid with 150 m between points. Like the riparian plots, the quantity of plots per watershed was proportional to the size of the watershed, with the largest watershed receiving 20 upland plots and the smallest receiving 10 (Table 1). Assuming a width of 7.5 m in riparian areas (see the Introduction), this resulted in a sampled area of approximately 3.7% for watershed P301 (an intermediate-sized watershed and stream) and approximately 0.26% in upland areas. Thus, riparian areas in our study may have been over-sampled relative to upland areas.

All plots were 10 × 20 m. Riparian plots were oriented with the long axis perpendicular to the stream channel, beginning at the stream's edge and extending 20 m away from the stream; orientations of upland plots were chosen randomly. Herbaceous plants and tree seedlings were sampled in 1 × 1-m quadrats located at 0, 5, and 10 m along the central axis of the plot. Riparian plots contained two quadrats at 0 m (at the stream's edge) to increase the likelihood of fully sampling the community in that diverse region. Riparian and upland plots were otherwise sampled with exactly the same protocol. In each quadrat, the cover by all vascular herbs was estimated, and counts of tree seedlings were made by species. Cover of woody species was estimated with the point-intercept method every 1 m along the plot's central axis in two layers: the shrub layer (< 2 m aboveground), and the canopy layer (≥~~2~~ m). All trees > 1 cm diam at breast height (dbh) were identified and measured. Locations were noted by estimating distance along the plot axis and noting the location on the left or right of the axis. Nomenclature of plant names follows Baldwin *et al*. (2012). A voucher collection of all vascular plant taxa identified is housed at the US Department of Agriculture (USDA), Forest Service, Pacific Southwest Research Station office, Fresno, CA. For a complete list of species and their scientific names, see the Supplemental Material (Appendix S1).

The multifaceted nature of KREW drove some of the sampling decisions for this study. The location of upland plots at existing soil grid points was done so that those plots could be analyzed with soil, nutrient, and other types of data collected at those locations. Also, the objective to characterize the transition had to be balanced with the broader objective of collecting plant community data across the entire KREW study site. Thus,

Table 1. Physical attributes of the eight watersheds sampled in this study, plus sample size of riparian and upland plots.

Watershed	Dominant vegetation	Elevation range (m)	Watershed area (ha)	Stream length (m)	No. upland plots	No. riparian plots
Providence Creek						
D102	Mixed-conifer	1,490–1,981	121	1,755	14	7
P304	Mixed-conifer	1,768–1,981	49	794	8*	4*
P303	Mixed-conifer	1,731–2,003	132	1,133	15	6
P301	Mixed-conifer	1,795–2,113	99	1,766	13	7
Bull Creek						
B201	Red fir	2,155–2,380	53	596	8*	0*
B203	Red fir	2,187–2,490	138	2,062	14	8
B204	Red fir	2,197–2,486	167	2,156	17	6*
T003	Red fir	2,051–2,465	228	3,171	19*	10

* A total of 15 plots that occurred entirely within meadows were excluded from analyses in this article because our focus was on riparian and upland forest communities.

plots were spread out more than they would have been had the sole objective been to characterize the transition of the plant community from riparian to upland areas. Extensive reconnaissance data, using species area curves, were collected on KREW sites before sampling (C.R.D., unpublished data), and those data suggested the full plant community in both riparian and upland areas was represented by our design.

DATA REDUCTION AND ANALYSES. To examine the transition from the riparian to upland herbaceous plant community, we compared mean species richness and cover in riparian quadrats at progressively farther locations of 0, 5, and 10 m from the stream's edge. We also compared mean richness and cover in 10-m riparian quadrats with the mean from all upland quadrats to examine similarities among plant species composition and cover in riparian and upland plots. For both species richness and cover, a generalized linear mixed model (GLMM) was fit with the 16 combinations of type (riparian and upland), creek (Bull Creek and Providence Creek), and quadrat location (0 m, 5 m, 10 m, and upland) as fixed effects, and watershed and "plot within watershed" as random factors, using a log link and negative binomial distribution. A Poisson distribution was initially considered, but the overdispersion factor estimates were much > 1.0, indicating an inadequate fit. Those analyses were performed with the GLIMMIX procedure in SAS software (version 9.4, SAS Institute, Cary, NC). For comparison of upland plots with riparian 10-m quadrats, we averaged the three quadrats within each upland plot and used the average in comparisons with the 10-m riparian quadrat in each plot. Treating the upland quadrats within each plot separately in this analysis would constitute pseudoreplication (Hurlbert 1984).

To qualitatively examine the transition of the herbaceous plant community, we determined the importance of the five most-dominant species for each quadrat location (riparian 0 m, 5 m, 10 m, and upland) and compared their importance at all other locations. In other words, for the five most-dominant species at a given quadrat location (*e.g.,* 0 m), we asked how their importance differed from all other quadrat locations (*e.g.,* 5 m, 10 m, and upland). To do that, we calculated the importance value (IV) for all herbaceous species by quadrat location, by calculating relative percentage of cover and the relative frequency, and then, averaged the two, resulting in IV200. We also performed nonmetric multidimensional scaling (NMDS) on the IV200 for the Providence Creek and Bull Creek herbaceous plant communities individually, using the metaMDS function of the vegan package version 2.3–3 (Oksanen *et al*. 2016) in R version 3.2.3 software (R Core Team 2015; R Foundation for Statistical Computing, Wien, Austria) and Bray as the distance measure, using two dimensions and the default in metaMDS of 20 random starts. We experimented with different distance measures, but Bray (Bray-Curtis) (Sørensen) provided the best separation of data; we also experimented with different numbers of dimensions. As a statistical test on community differences, we performed runs of the multiple response permutation procedure

(MRPP) with a Euclidian dissimilarity index on raw cover values for herbs in riparian 10-m quadrats *vs*. upland quadrats, also with the vegan package in R software. In those analyses, the upland quadrat locations could not be averaged because the analysis was on raw cover instead of IV200. Therefore, we ran analyses on the 10-m riparian quadrats against each of the three upland locations (also 0, 5, and 10 m along the plot's sampling axis).

To compare forest structure in the riparian forest with the upland forest, we compared stem density (trees ha^{-1}), basal area (m^2 ha^{-1}) of stems, and quadratic mean diameter (QMD) for both live trees and snags (*i.e*., all standing dead trees). To see whether forest structure varied with increasing distance from the stream within riparian forests, we subdivided riparian plots into two 10 × 10-m sections: the first (near-stream), starting at 0 m (adjacent to the stream) and extending to 10 m; and the second (far-stream), starting at 10 m and extending to 20 m. We then compared both near-stream and far-stream portions with upland plots (upland plots were not subdivided). Again, we constructed a single GLMM for each of the three measures (density, basal area, and QMD), using plot as a random effect and creek + half + creek × one half as the fixed effect. For density, a Poisson distribution with a log link was used on the snags data set, but a negative binomial distribution with a log link was used for live trees because the additional variability was beyond what Poisson could appropriately describe. Trees per hectare used the number of stems as the dependent variable, with the log of the plot area as an offset to correct for slope. Basal area and QMD used an identity link with a normal distribution and no offset. All tests were performed in SAS 9.4 using the PROC GLIMMIX procedure.

We also calculated importance values for shrub and tree species in near-stream, far-stream, and upland plots. Shrub importance values were based on relative cover along the shrub layer of the line-intercept and on relative frequency. Tree importance values were based on relative density, relative basal area (*i.e.,* cover), and relative frequency.

Results. Herbaceous species richness and cover declined sharply from 0- to 5-m quadrat locations in riparian plots for both Providence Creek and Bull Creek watersheds and were statistically significant for richness in both Providence and Bull creeks (GLMM, $P < 0.001$ for both) but were significant for cover only in Bull Creek ($P < 0.001$; Fig. 3). Richness and cover both declined from 5- to 10-m locations as well but were nonsignificant. Richness and cover were markedly lower in upland quadrats for both Providence Creek and Bull Creek, with significant differences for richness in Bull Creek ($P = 0.004$) and for cover in both Providence ($P < 0.001$) and Bull ($P < 0.001$) creeks between upland and 10-m riparian locations. In Providence Creek, richness dropped from a mean of 9.5 species $quadrat^{-1}$ next to the stream (riparian 0-m quadrat) to 3.9 at 10-m riparian quadrats, then down to 2.4 in upland quadrats. The range in Bull Creek was greater, dropping from 11.7 to 3.1 species $quadrat^{-1}$ from 0 to 10-m riparian quadrats, but down to 1.5 in upland quadrats. The difference in total cover between 10-m riparian quadrats and upland quadrats was particularly striking, with Providence and Bull creeks 10-m quadrats averaging 21.4% and 28.6% cover, respectively, whereas upland quadrats averaged 4.5% and 4.4%, respectively (Fig. 3).

Analyses of herb composition also supported different communities at 10-m riparian locations *vs*. upland locations. Herbaceous species that dominated in 0-, 5-, and 10-m riparian quadrats were absent or of low importance in upland plots. Conversely, species that dominated upland plots were of low importance or absent in riparian plots (Fig. 4, 5). The MRPP analyses suggested that the 10-m riparian quadrat location was less distinct from other riparian quadrats than upland quadrats in Providence Creek. In Bull Creek, riparian 10-m quadrat communities were less different from riparian 5-m quadrats, but were equally distinct from both 0-m quadrats and upland quadrats (Table 2).

Further support for the separation of upland locations from 10-m riparian locations comes from the NMDS of IV200 in the three riparian locations *vs*. the averaged upland quadrats (Fig. 6). Ordination results for both creeks were highly stable, with final stresses near zero for a two-axis solution; using a third axis, thus, provided no more information. The graphs demonstrate that upland plots separate from all riparian plots along axis 1, and the riparian plots separate from each other along axis 2 (Fig. 6). That strongly supports the

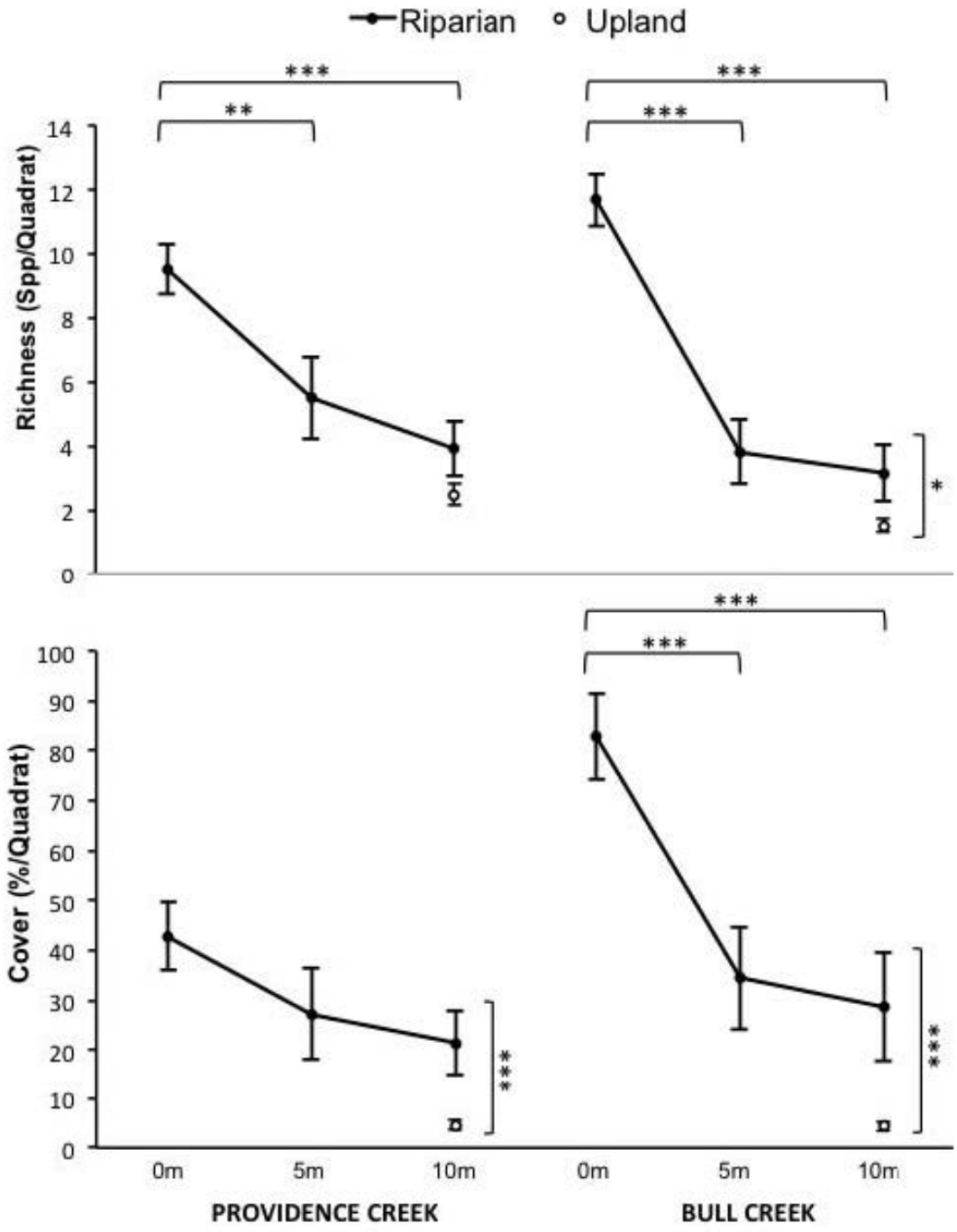

FIG. 3. Transition from the stream's edge showing mean species richness and cover of herbaceous species found in quadrats at 0 m, 5 m, and 10 m from the stream's edge, compared with that of quadrats in upland plots. Statistically significant results (GLMM single model) are indicated by * $P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

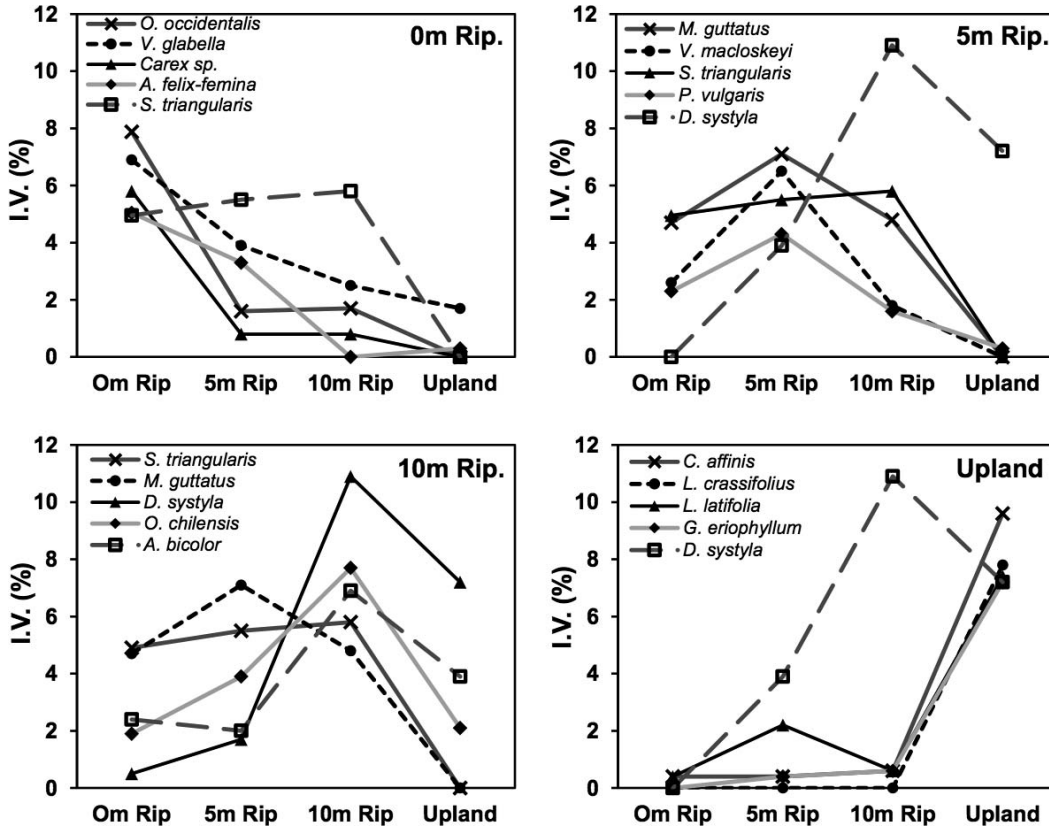

FIG. 4. Providence Creek trends in dominance for quadrats located at the stream's edge (0 m Rip), 5 m from the edge (5 m Rip), 10 m from the edge (10 m Rip) and upland plots (Upland) for the five most-dominant herbaceous species at each location. Data are importance values (I.V.), calculated from percentage of cover and frequency for each species.

conclusion that composition in riparian quadrat locations was much more similar to each other than it was to upland quadrats. Herbaceous taxa indicative of upland locations in Providence Creek included *Eriogonum nudum* (Benth.), *Gayophytum diffusum* Torr. & A. Gray, *Gayophytum eriospermum* Coville, *Hemizonella minima* (A. Gray) A. Gray, and *Viola purpurea* Kellogg. Taxa indicative of 0-m riparian locations in Providence Creek included *Epilobium* spp., *Luzula parviflora* (Ehrh.) Desv., *Mimulus cardinalis* Benth., and *Bistorta bistortoides* (Pursh) Small. Taxa indicative of upland areas in Bull Creek included *Stipa occidentalis* S. Watson, *Elymus elymoides* (Raf.) Swezey, *Eriogonum* spp., *Lupinus fulcratus* Greene, and *Streptanthus tortuosus* Kellogg. Taxa indicative of 0-m riparian locations in Bull Creek included *Athyrium filix-femina* (L.) Roth, *Circaea alpina* L., *Heracleum maximum* W. Bartram, and *Veronica* spp. Many species are associated with 5- or 10-m riparian areas in both creeks but included *Senecio triangularis* L., *Adenocaulon bicolor* Hook., and *Mimulus guttatus* DC in Providence Creek, and *Castilleja applegatei* Fernald, *Juncus oxymeris* Engelm., *Ligusticum grayi* J.M. Coult. & Rose, and *Maianthemum racemosum* (L.) Link in Bull Creek (Fig. 6; Supplemental Material [Appendix S2]).

Density of live trees was greater in riparian forest plots than in upland forest plots in Providence Creek (mixed-conifer forest). Both near- and far-stream forests were denser than in upland forests, but differences were statistically significant only for the far-stream riparian forests *vs*. upland forest (GLMM; $P = 0.004$), a difference of more than 500 trees ha^{-1} (Fig. 7). For Bull Creek

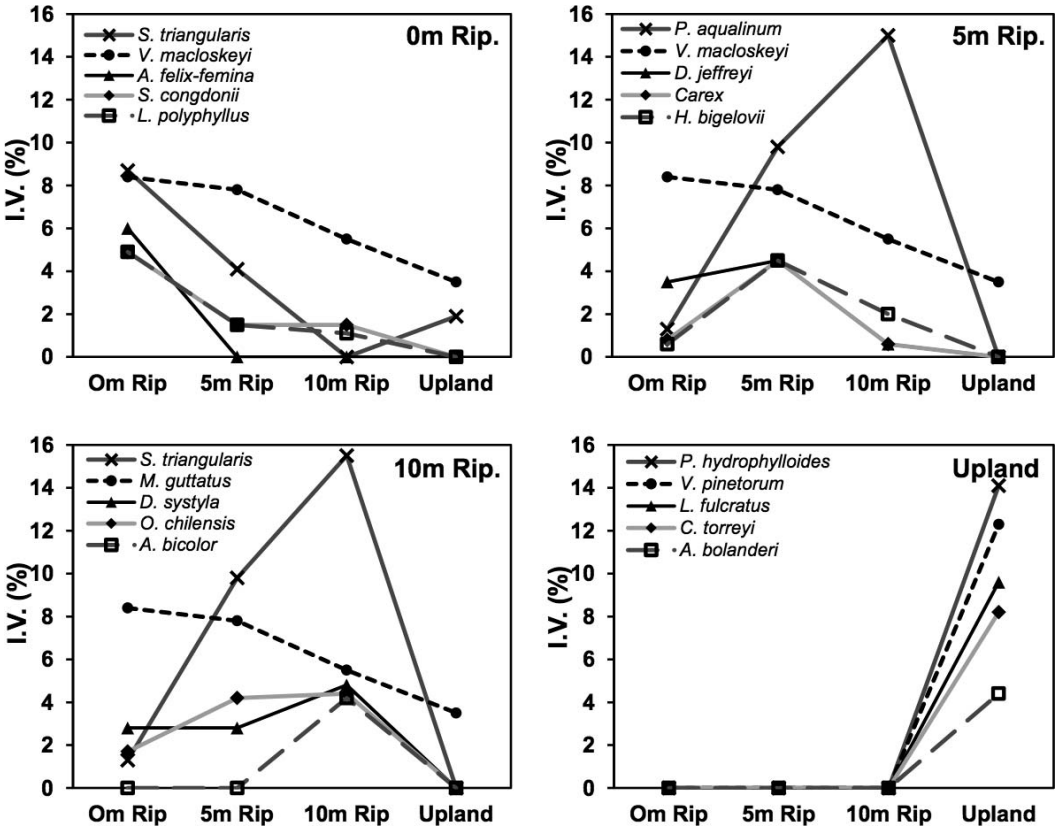

FIG. 5. Bull Creek trends in dominance for quadrats located at the stream's edge (0 m Rip), 5 m from the edge (5 m Rip), 10 m from the edge (10 m Rip) and upland plots (Upland) for the five most dominant herbaceous species at each location. Data are importance values (I.V.), calculated from percent cover and frequency for each species.

(mostly red fir forest), there was very little difference in live-tree density among near-stream (0–10 m) riparian, far-stream (10–20 m), and upland plots. Far-stream locations in Providence Creek had markedly higher snag densities than either near-stream or upland locations and was statistically significant for near-stream *vs*. far-stream riparian locations ($P = 0.004$). Live tree basal area was significantly greater in far-stream riparian locations than in either near-stream or upland locations for both Providence Creek (*vs*. near-stream: $P = 0.045$; *vs*. upland: $P = 0.021$), and Bull Creek (*vs*. near-stream: $P = 0.028$; *vs*. upland: $P = 0.012$). Snags followed similar trends, but differences were not significant. Quadratic mean diameter was highest in upland plots for Providence Creek and far-stream plots for Bull Creek for both live trees and snags, although all differences were nonsignificant. Thus, the far-

Table 2. Multiple response permutation procedure results on herbaceous communities for riparian 10 meter quadrats (Rip 10 m) compared with upland quadrats (Upl 0 m, Upl 5 m, Upl 10 m), and riparian 5 m (Rip 5 m) and 0 m [Rip 0 m L (left) & Rip 0 m R (right)] quadrats. Analysis was carried out on percentage of cover.

Comparison	A	*P* value
Providence creek		
Rip 10 m *vs*. Upl 0 m	0.0284	0.002
Rip 10 m *vs*. Upl 5 m	0.0168	0.012
Rip 10 m *vs*. Upl 10 m	0.0173	0.014
Rip 10 m *vs*. Rip 5 m	−0.0005	0.434
Rip 10 m *vs*. Rip 0 m L	0.0133	0.035
Rip 10 m *vs*. Rip 0 m R	0.0074	0.100
Bull creek		
Rip 10 m *vs*. Upl 0 m	0.0323	0.002
Rip 10 m *vs*. Upl 5 m	0.0295	0.001
Rip 10 m *vs*. Upl 10 m	0.0284	0.002
Rip 10 m *vs*. Rip 5 m	−0.0086	0.887
Rip 10 m *vs*. Rip 0 m L	0.0432	0.001
Rip 10 m *vs*. Rip 0 m R	0.0418	0.001

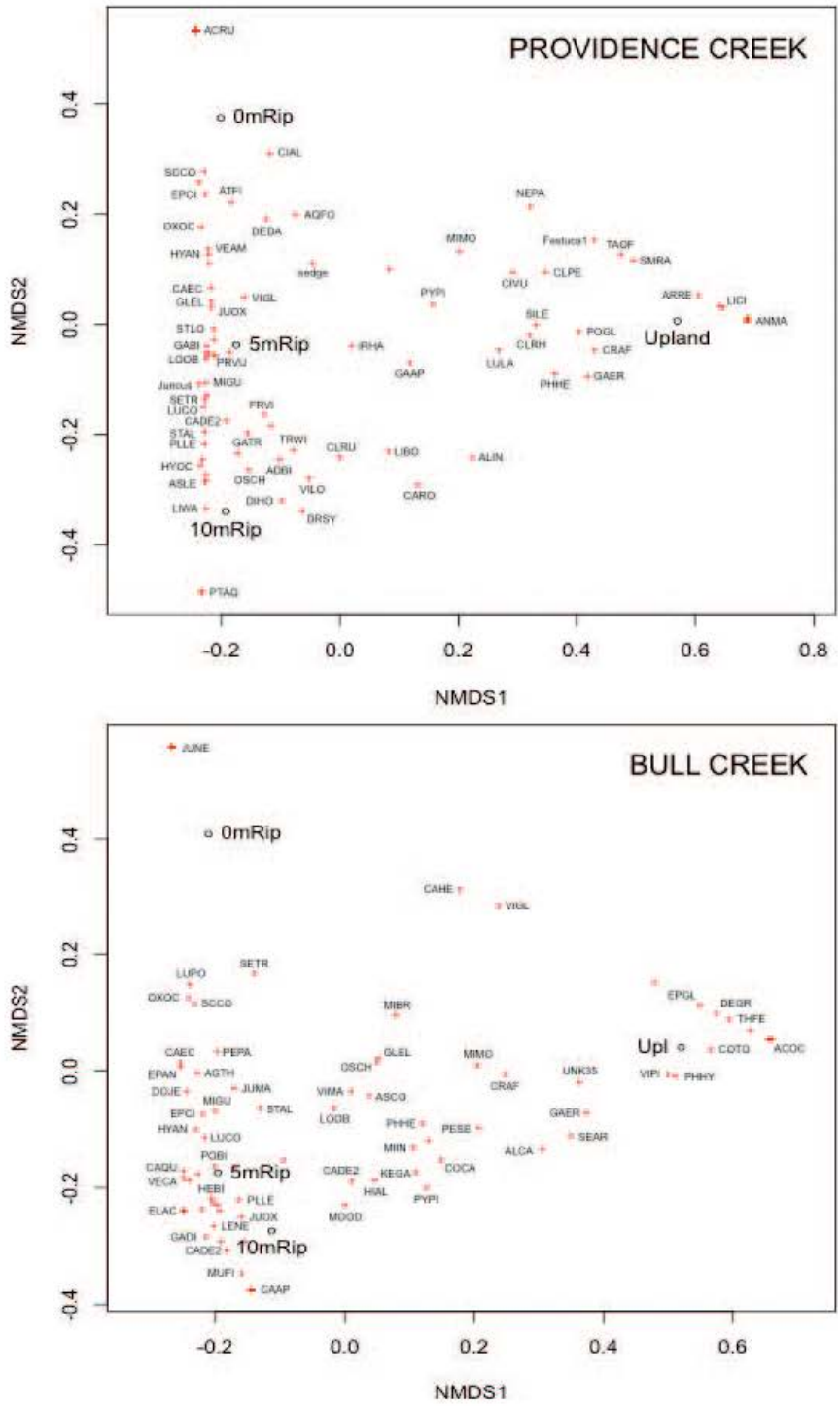

FIG. 6. Plot of nonmetric multidimensional scaling results for the Providence Creek and Bull Creek herbaceous plant communities based on IV200 values calculated as an average of relative cover and relative frequency across the quadrat location. Scientific names associated with species codes can be found in Appendix S1. Additional species scores can be found in Appendix S2.

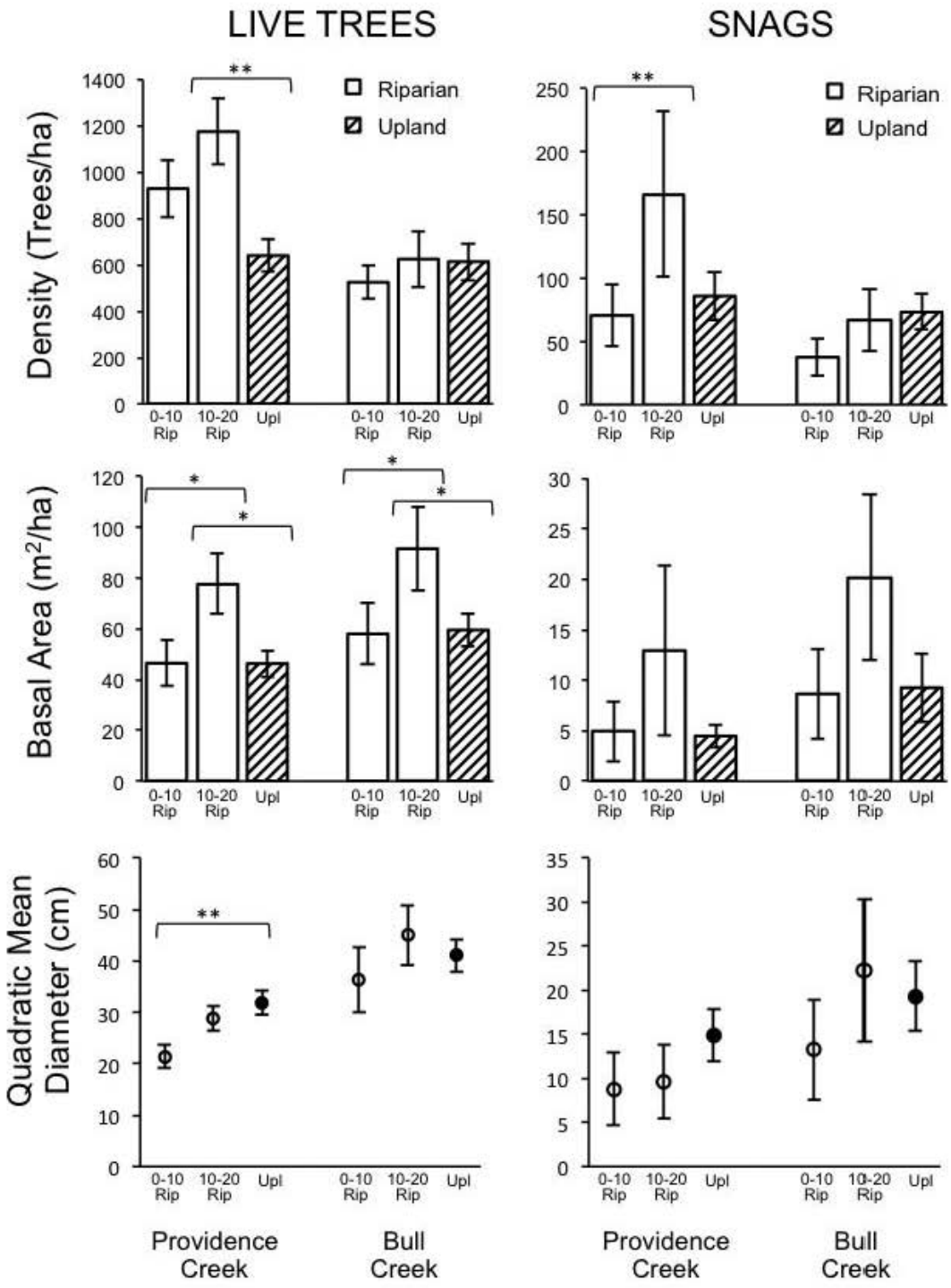

FIG. 7. Density, basal area, and quadratic mean diameter for live trees and snags in 0 to 10-m portions of riparian plots (0–10 Rip), 10 to 20-m portions of riparian plots (10–20 Rip), and upland plots (Upl) for Providence Creek and Bull Creek, separately. Statistically significant results (GLMM single model) are indicated by * $P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

stream riparian forests were denser than both near-stream riparian and upland forests in mixed-conifer forest and had higher basal area than both in mixed-conifer and red fir forests (Fig. 7).

In Providence Creek, the importance of *A. concolor* changed very little from near-stream to far-stream to upland forest (Table 3). Importance of *C. decurrens*, however, decreased along this gradient, from 44.6% in near-stream forests to 29.1% in upland forests. Dominance of *P. lambertiana* increased from riparian to upland forests, comprising only 3.6% of near-stream riparian forests, but 14.6% of upland forests. Composition of shrub species shifted from greater dominance by *Ribes nevadense* Kellogg, *Ribes roezlii* Regel, and *Chamaebatia foliosa* Benth. in riparian forests, to dominance by *Ceanothus cordulatus* Kellogg and *Arctostaphylos patula* Greene in upland forests (Table 3).

In Bull Creek, dominance by *A. magnifica* changed very little from near-stream to far-stream to upland forest (similar to *A. concolor* in Providence Creek). Importance of *A. concolor* increased along that gradient, from 14.4% in near-stream forest to 33.4% in upland forest (Table 3), reflecting its increased dominance on drier sites relative to *A. magnifica* observed elsewhere. Dominance by *Chrysolepis sempervirens* (Kellogg) Hjelmqvist in the shrub layer was much greater (+ 24.6%) in upland forest than it was riparian forest, whereas dominance by *Symphoricarpos mollis* Nutt., *Rhododendron columbianum* (Piper) Harmaja, *Ribes nevadense,* and *Ribes viscosissimum* Pursh was greater in riparian forest (Table 3).

Discussion. Our results strongly suggest that the riparian, herbaceous community 10 m from the stream was very different from the upland community and was actually more similar to the riparian community 0 and 5 m from the stream (Fig. 3–6), causing us to reject hypothesis 1 (hypothesis 1: the riparian plant community beyond 7.5 m from the stream should be more similar to the upland plant community than to the riparian plant communities closer to the stream). The boundary of the riparian community clearly extended beyond 10 m from the stream in our study site. Although results for forest structure were less consistent, they suggest that riparian forests have a different structure (denser, with smaller trees and more snags) than upland forests (Fig. 7), but that trend was stronger in the Providence Creek watersheds than it was in Bull Creek. Thus, we can reject hypothesis 2 (hypothesis 2: because of the similar fire histories of riparian and nearby upland regions, the riparian zones will have a forest structure similar to upland forest) for Providence Creek and tentatively accept it for Bull Creek.

Our finding that the herbaceous community at 10 m from the stream was still significantly different from the upland community was particularly surprising, given that the canopy composition is similar (Table 3) and the previous finding that the microclimate beyond 7.5 m from the stream was not statistically different from upland locations (Rambo and North 2008). Rambo and North (2008), however, did not measure soil moisture, which may have a greater influence on plant distributions in the Sierra Nevada than in non-Mediterranean mountain ranges because of its ameliorating effect on the long, summer dry season (Peterson 1998). Herbaceous plants vary at finer scales than woody plants do and often respond to environmental gradients and disturbances differently (Gilliam 2007). In riparian areas in northern Europe, Decocq (2002) found that riparian herbs responded primarily to soil chemistry and secondarily to light availability and that different layers of the forest responded differently to a variety of gradients. Similarly, the herbs and woody plants across KREW (both riparian and upland) appear to be operating at two different scales on the landscape, in response to the influence of the stream. An interesting example of an herbaceous plant in our study that prefers the 10-m riparian zone was *Pteridium aquilinum* (L.) Kuhn (brackenfern). It is often found in dry soils yet in close proximity to streams (C.R.D., personal observation), and our ordination analysis supported that; the brackenfern was strongly associated with the 10-m riparian quadrat location (Fig. 6; Appendix S2). Perhaps brackenfern could be used as an indicator of locations that have the appearance of upland communities but are still influenced by the stream in some way, possibly by elevated soil moisture relative to upland locations.

Our results are consistent with the conclusion of Sabo *et al.* (2005), that there is high species turnover between riparian and upland plant communities. However, unlike Sabo *et al.*

Table 3. Composition of trees and shrubs in 0–10 m and 10–20 m riparian and upland plots.

	0 to 10 m Riparian				10 to 20 m Riparian				Upland				
	Rel. Density (%)	Rel. Cover (%)	Rel. Freq. (%)	I.V.	Rel. Density (%)	Rel. Cover (%)	Rel. Freq. (%)	I.V.	Rel. Density (%)	Rel. Cover (%)	Rel. Freq. (%)	I.V.	Change from Rip to Upland
PROVIDENCE CREEK													
Trees													
Abies concolor	39.0	42.9	29.6	**37.2**	39.7	51.8	26.0	**39.2**	43.4	40.7	33.1	**39.1**	0.9
Calocedrus decurrens	43.6	51.3	38.9	**44.6**	48.4	32.4	28.8	**36.5**	29.3	30.4	27.7	**29.1**	-11.4
Cornus nuttallii	10.1	1.2	16.7	**9.3**	1.8	0.2	6.8	**2.9**	5.1	0.2	5.4	**3.6**	-2.6
Cornus sericea	1.4	0.0	1.9	**1.1**					0.5	0.0	0.8	**0.4**	-0.7
Corylus cornuta	1.8	0.0	1.9	**1.2**	1.8	0.2	6.8	**2.9**	0.2	0.0	0.8	**0.3**	-1.8
Pinus jeffreyi									0.3	1.1	1.5	**1.0**	1.0
Pinus lambertiana	1.4	3.9	5.6	**3.6**	1.8	12.3	6.8	**7.0**	6.3	22.1	15.4	**14.6**	9.3
Pinus ponderosa					1.4	2.4	5.5	**3.1**	3.7	4.5	5.4	**4.5**	1.4
Prunus emarginata									6.9	0.1	1.5	**2.8**	2.8
Quercus chysolepis	1.4	0.1	1.9	**1.1**	2.5	0.4	9.6	**4.2**	2.5	0.3	3.1	**2.0**	-0.6
Quercus kelloggii	0.9	0.0	1.9	**0.9**	0.7	0.5	2.7	**1.3**	1.5	0.5	4.6	**2.2**	1.1
Shrubs													
Arctostaphylos patula										18.8	14.3	**16.6**	16.6
Ceanothus cordulatus		25.0	9.1	**17.0**		16.1	7.7	**11.9**		31.8	25.7	**28.8**	14.4
Ceanothus integerrimus										8.5	5.7	**7.1**	8.4
Ceanothus parvifolius										2.7	1.4	**2.1**	2.4
Chamaebatia foliosa		25.0	18.2	**21.6**		19.4	15.4	**17.4**		10.8	8.6	**9.7**	-9.8
Chrysolepis sempervirens										1.4	3.8	**2.6**	2.6
Rhamnus rubra										1.4	3.8	**2.6**	2.6
Ribes nevadense		25.0	45.4	**35.2**		6.5	7.7	**7.1**		4.9	7.1	**6.0**	-15.2
Ribes roezlii		20.8	18.2	**19.5**		38.7	46.2	**42.4**		12.6	20.0	**16.3**	-14.7
Rosa bridgesii		4.2	9.1	**6.6**		3.2	7.7	**5.5**		3.6	4.3	**3.9**	-2.2
Symphoricarpos mollis						9.7	7.7	**8.7**		3.6	7.1	**5.4**	-3.3
BULL CREEK													
Abies concolor	13.5	10.6	19.0	**14.4**	14.7	31.5	26.5	**24.2**	33.4	32.6	34.1	**33.4**	14.1
Abies magnifica	65.1	83.9	47.6	**65.5**	64.0	63.6	52.9	**60.2**	63.5	61.0	53.4	**59.3**	-3.6
Calocedrus decurrens									1.8	1.3	2.3	**1.8**	1.8
Corylus cornuta					1.3	0.0	2.9	**1.4**	0.3	0.0	2.3	**0.9**	-0.6
Pinus contorta var. murrayana	12.7	3.1	9.5	**8.4**	13.3	1.9	8.8	**8.0**					-8.2
Pinus jeffreyi	1.6	2.0	2.4	**2.0**	5.3	1.6	2.9	**3.3**	0.1	0.2	1.1	**0.5**	-2.2
Pinus lambertiana	1.6	0.3	4.8	**2.2**	1.3	1.4	5.9	**2.9**	0.7	4.9	5.7	**3.7**	1.2
Salix	4.0	0.0	11.9	**5.3**					0.1	0.0	1.1	**0.4**	-4.9
Shrubs													
Arctostaphylos nevadensis						8.3	9.1	**8.7**		16.5	20.4	**18.5**	9.8
Ceanothus cordulatus		30.4	33.3	**31.9**		16.7	27.3	**22.0**		31.5	22.4	**27.0**	0.1
Chrysolepis sempervirens		30.4	11.1	**20.8**		8.3	18.2	**13.3**		46.5	36.7	**41.6**	24.6
Ledum glandulosum		4.3	11.1	**7.7**		16.7	9.1	**12.9**					-10.3
Ribes nevadense		17.4	11.1	**14.3**		8.3	9.1	**8.7**		1.0	4.1	**2.5**	-9.0
Ribes viscosissimum		4.3	11.1	**7.7**		8.3	18.2	**13.3**		1.5	4.1	**2.5**	-8.0
Symphoricarpos mollis		13.0	22.2	**17.6**		29.2	9.1	**19.1**		1.5	6.1	**3.8**	-14.6
Vaccinium uliginosum						4.2	9.1	**6.6**					-6.6

(2005), our data also suggest riparian areas are more species rich, with three to four times as many herbaceous species as upland areas (Fig. 3). Sabo *et al*. (2005) mentioned that turnover patterns between riparian and upland areas were stronger in dry climates. That pattern may be particularly strong on small, first-order streams, such as those in KREW (Fig. 2), and appears to be strongest in our higher-elevation, more-open forests in Bull Creek.

The finding that Providence Creek riparian forests have higher stem density than the nearby upland forest has was supported by other studies from the Sierra Nevada (Van de Water and North 2011) and the Rocky Mountains (Dwire *et al*. 2015) but was different from the more-arid regions of the Intermountain West (Dwire and Kauffman 2003). Interestingly, the near-stream riparian areas in our study had about the same tree density and basal area as our upland sites and also

had the smallest trees. That finding probably reflects the fact that disturbances, such as flooding, soil erosion, and stream channel shifts are more common near the stream (Naiman *et al*. 2001). The riparian far-stream portions on the other hand, may be an ideal location for trees, farther from the instability of the stream, but still close enough to benefit from higher humidity and soil moisture and thus reduced drought stress. The amount of cover from down dead wood also peaked at the 5-m location (data not shown). The fact that Bull Creek riparian and upland forests were more similar in structure could reflect their different forest types and elevations. Bull Creek is more dominated by red fir forest, which historically had longer fire return intervals (Van de Water and Safford 2011) and thus, even if untreated, riparian forests in Bull Creek may be closer to their upland counterparts because their fire regime is less altered than the mixed-conifer forests of Providence Creek.

What does this mean for management of riparian zone vegetation, at least for middle elevations of the Sierra Nevada? Similar to many upland areas of the range, riparian forests are probably also experiencing elevated live and dead fire fuels, and both areas appear to have burned at similar frequencies in the past (Kobziar and McBride 2006, Van de Water and North 2011). This suggests that riparian areas should be managed for fuels reduction and forest restoration similar to their upland counterparts, or, although perhaps unlikely, be allowed to burn naturally (Hunsaker and Long 2014). However, we conclude here that the riparian plant community extends more than 10 m away from narrow headwater streams, into what may appear, to the casual observer, to be dry upland forest. Our data suggest that a management plan for the southern Sierra headwaters that includes protection of riparian herbs as a priority should include a buffer zone in which mechanical treatment is not allowed. That zone could, however, be narrower than the current 91 m for perennial streams in the Sierra Nevada. Or, if fuels reduction is the highest priority, then, perhaps no buffer zone of protection is necessary; restoration of the forests and their fire regime across the entire watershed might be more critical. Riparian plants, including herbaceous species, have many adaptations to fire and have been shown to recover quickly after disturbance (Dwire and Kauffman 2003). In some forests, one or two prescribed burns may significantly restore the health and resilience of riparian areas without altering the community over the long term. Previous research on prescribed burning in riparian zones suggests the herbaceous community will change after fire (Bêche *et al*. 2005), but that change may be short lived. What we can say is that more research is needed to understand the balance between the protection of the diverse riparian community and restoring its fire regime. We hope to bring clarity to this important topic with the completion of understory prescribed burn treatments on KREW, and the subsequent comparison of pretreatment and posttreatment plant-composition data.

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