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Landscape controls on the distribution and ecohydrology of central Oregon springs

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Abstract

Small springs in semiarid landscapes are essential for maintaining aquatic biodiversity and supporting livestock grazing operations. However, little is known about controls on the distribution and physical characteristics of small springs, the aquatic species they support, or their sensitivity to disturbance. We address this information gap in the Crooked River subbasin, a tributary of the Deschutes River in Oregon. We conducted spatial analyses on 2,519 mapped springs to investigate the influence of landscape controls (precipitation and bedrock permeability) on spring density in the Crooked River subbasin and the adjacent Upper Deschutes subbasin. Spring density was highest in areas of low bedrock permeability ($P < 0.0001$) and high annual precipitation ($P < 0.0001$). We suggest that the high density of small springs on low-permeability bedrock indicates that these springs generally have short, shallow flow paths and thus may be susceptible to forecasted climate changes. A survey of 137 springs in the Crooked River subbasin revealed the hydrogeologic setting affects spring discharge type ($P = 0.017$), temperature ($P = 0.011$), and pH ($P = 0.026$). We found a high frequency of anthropogenic impacts on springs: 95% of diffuse-discharge springs and 79% of discrete-discharge springs were disturbed by livestock grazing. Species inventories at 10 of the most intact surveyed springs confirm that small springs are biologically diverse, with 151 total species of plants and 135 total taxa of macroinvertebrates. Springs in the Crooked River subbasin are ecologically important habitats but require careful management to protect against livestock disturbance and development.

KEYWORDS

disturbance, groundwater, macroinvertebrate diversity, Oregon, permeability, plant diversity, springs

1 | INTRODUCTION

Springs in semiarid environments and their associated biota are “keystone ecosystems” because their ecological importance is disproportionately large in comparison with their small size (Perla & Stevens, 2008). In many arid and semiarid environments, springs are the only perennial source of water. These groundwater-dependent ecosystems are among the most biologically diverse habitats in the semiarid western United States (Shepard, 1993). Springs provide habitat for many endemic (Davis, Pavlova, Thompson, & Sunnocks, 2013), obligate (Anderson & Anderson, 1995), and rare aquatic species (Blevins & Aldous, 2011), a fact generally attributed to their consistent water quality characteristics and flow (Cantonati, Fureder, Gerecke, Juttner, & Cox, 2012). Springs also are critically important water and forage sources for nonaquatic wildlife and migratory birds (Sada et al., 2001).

Springs historically have been impacted by anthropocentric uses without regard for ecological integrity or preservation of flow

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(Unmack & Minckley, 2008). They often are developed for domestic use, irrigation, livestock, or game animals, particularly in the arid and semiarid western United States (Sada et al., 2001). For example, in two separate studies in Nevada, 60% of 511 surveyed springs in the north and 78% of 45 surveyed springs in the south had been disturbed by diversions for livestock use or other development (Sada, Fleishman, & Murphy, 2005; Sada, Vinyard, & Hershler, 1992). Disturbance of spring habitat due to water diversions is the most common threat influencing the abundance and distribution of aquatic macroinvertebrate species in the Great Basin of Oregon, Utah, and Nevada (Sada & Vinyard, 2002). The extinctions of some species, such as the *Pyrgulopsis ruinosa* spring snail, have been attributed directly to water diversions for livestock use (Hershler, 1998). Development of a spring for livestock typically consists of excavating the spring and installing a collection box and piping water to an impoundment, trough, or reservoir. When springs are developed, the resulting desiccation of the spring habitat can eradicate their aquatic assemblages (e.g., Hershler, 1998). Furthermore, developed and undeveloped springs used by livestock and wild ungulates are impacted by grazing of riparian vegetation, trampling and compaction, and water quality degradation due to faeces (Sada et al., 2001).

The low-discharge springs commonly found in the semiarid western United States have few legal protections for their water sources or the habitat itself (Aldous & Bach, 2011). Under the Clean Water Act, small springs with intermittent or no surface flow connections to perennial rivers are considered “geographically isolated wetlands.” There is an ongoing debate as to whether these types of waters warrant state and federal regulation (i.e., are considered jurisdictional). Springs can receive protection under the Endangered Species Act if they harbour species listed as threatened or endangered. Although listed species appear to be relatively common in groundwater-dependent ecosystems (Blevins & Aldous, 2011), the distribution of these species is often unknown because there are so few spring surveys. Protections under state law can be equally minimal. For example, under Oregon water law, water developments on small springs rarely require a water right because the volume of water extracted is below the state's threshold for permitting, or the natural flow from the spring infiltrates into the soil before crossing a property line, which exempts the development from permitting requirements (Oregon Water Resources Department, 2013).

Although more agencies and land managers are recognizing the importance of preserving spring habitat (e.g., USDA Forest Service, 2012a, 2012b), critical information gaps hinder the ability of resource managers to make informed decisions, particularly for low-discharge springs. Spring mapping on older maps is of variable quality and commonly underestimates the actual number of springs (Junghans, Springer, Stevens, & Ledbetter, 2016). Most spring maps and geodatasets lack information on recharge area, discharge rate, discharge type (e.g., diffuse-discharge seeps or discrete-discharge gushets), water chemistry, whether they are fed by regional versus local flow systems, and other fundamental characteristics that affect habitat type and ecology. Understanding the flow systems feeding the springs is needed because springs have different characteristics based on the extent of the flow path, size of the recharge area, and length of residence time (Manga, 1999; Tóth, 1963). For example, groundwater in regional flow systems in the Deschutes Basin, Oregon—which includes the study area—follows long flow paths (tens of kilometres) with potentially large recharge areas, has long residence times (centuries), and shows small seasonal variations in discharge relative to mean flow (Gannett, Manga, & Lite, 2003; Manga, 1996, 1997, 1999; Waibel, Gannett, Chang, & Hulbe, 2013). Local flow systems, in contrast, can have very short flow paths (tens of meters), small recharge areas, short residence times, and large seasonal fluctuations in flow. These differences in flow system scale are likely to affect how resilient springs are to climate change. Spring management is problematic in the context of these information gaps because “one-size-fits-all” management plans are insufficient to appropriately protect the wide range of spring habitat types. A more complete understanding of the link between springs and their landscape context is needed to facilitate long-term management of these sensitive ecosystems.

Despite the ecological importance of springs, their vulnerability to development, and lack of legal protections, there have been few studies at the landscape scale documenting controls on their distribution, site-specific characteristics, or extent of disturbance and development (Perla & Stevens, 2008). The lack of spring surveys is particularly true in Oregon, which has the highest density of springs in the United States (Stevens & Meretsky, 2008) at 0.12 springs/km^2 (J. Brown, Wyers, Bach, & Aldous, 2009). Field research on spring ecosystems in the western United States has been limited primarily to more arid ecoregions in the south-west (e.g., Flora, 2004; Sada et al., 2005; Sada & Vinyard, 2002). Due to the scarcity of field data, there is a need to develop methods to use widely available geospatial information to gain insights into factors controlling the spatial distribution, hydrology, and ecology of springs across the landscape. Such landscape-scale methods could be used to inform management decisions and to prioritize springs for protection and restoration in areas lacking site-scale information.

In this study, we evaluate the relationship between landscape-scale geospatial information and field observations to better understand the hydrogeologic setting of springs in the Crooked River subbasin in central Oregon and how they are likely to respond to major stressors. The hydrogeologic setting is a determinant of spring distributions, and it influences groundwater flow paths, spring type (Springer & Stevens, 2009), water chemistry, discharge rates, and the response of springs to seasonal and longer term climate forcing (Bedford, 1996). These fundamental spring characteristics, in turn, influence species composition and ecosystem services of associated ecosystems and their vulnerability (Godwin, Shallenberger, Leopold, & Bedford, 2002). The Crooked River subbasin is representative of conditions encountered in semiarid landscapes throughout the western United States because it has a high density of mapped springs occurring across a large range of annual precipitation, elevation, and bedrock characteristics. The objectives of this study were (a) describe the landscape conditions and hydrogeologic settings in which springs are found; (b) determine the relationships between different hydrogeologic settings and spring characteristics including spring density, discharge type, and water chemistry; (c) better understand the extent and nature of ecological stressors to springs in semiarid landscapes; and (d) test assumptions that these semiarid springs support high biodiversity. We employ spatial analysis of existing and derived landscape-scale data for springs in both the Upper Deschutes and the Crooked River subbasins to address the first objective. The remaining three objectives were addressed by a field inventory of springs in the Crooked River subbasin.

2 | METHODS

2.1 | Study area

This study is focused on the Crooked River subbasin (Hydrologic Unit Code 8 [HUC8] subbasins: 17070303, 17070304, and 17070305), a catchment within the Deschutes River Basin, which encompasses 11,850 km^2 of central Oregon (Figure 1). Elevations in the Crooked River subbasin range from about 500 to 1,800 m. Mean annual discharge of the Crooked River is 43.6 m^3 s^{-1} near its confluence with the Deschutes River (U.S. Geological Survey [USGS] gage 14087400; USGS, 2017). Along the lower 22 km of the Crooked River, there is regional groundwater discharge of about 28 m^3 s^{-1}, providing roughly two thirds of the mean annual flow (Gannett & Lite, 2004; Gannett, Lite, Morgan, & Collins, 2001; James, Manga, Rose, & Hudson, 2000). Above this lower reach, there are large seasonal flow variations characteristic of a run-off-dominated stream system, with mean flows ranging from 42.7 m^3 s^{-1} in April to 0.31 m^3 s^{-1} in August (USGS gage 14080500, period of record 1941–1959 prior to construction of major impoundments; Friday & Miller, 1984).

Annual precipitation in the Crooked River subbasin ranges from about 200 mm year^{-1} at the lowest elevations near the confluence with the Deschutes River to more than 1,000 mm year^{-1} at highest elevations in the Ochoco Mountains (PRISM Climate Group, 2017). Most of the basin receives between 200 and 400 mm year^{-1}, with approximately 80% of the precipitation falling as snow during winter months at higher elevations (Natural Resources Conservation Service, 2017; Western Regional Climate Center, 2017). Minimum 30-year normal temperatures across the basin range from −2.9°C at higher elevations to 1.7°C at lower elevations, whereas maximum 30-year normal temperatures range from 16.8°C at the lowest elevations to 10.1°C at the highest elevations (PRISM Climate Group, 2017).

Vegetation at the lowest elevations in the Crooked River subbasin is dominated by the *Juniperus occidentalis* forest zone, whereas forests of the *Pinus ponderosa* zone dominate at higher elevations (Franklin & Dyrness, 1988). Mixed Ponderosa, Douglas fir, and true fir forests occur in places at highest elevations (Loy, 2001). Cultivated agriculture is largely restricted to valley bottoms, although much of the remainder of the basin, including the forested areas, is used for livestock grazing.

Because of the high density of springs, field components of this study focused on the Crooked River subbasin of the Deschutes River Basin (Figure 1), for which a database of mapped springs was compiled using published spring locations from the National Hydrography Dataset (USGS, 2013). However, for an initial spatial analysis, springs in the adjacent Upper Deschutes subbasin were included from the same data source.

The Deschutes River Basin, which includes the Crooked River and Upper Deschutes subbasins, is dominated by volcanic deposits such as lava flows, vent complexes, pyroclastic deposits, debris flows, and volcanic-derived sediment ranging in age from Oligocene to Holocene, with small areas of pre-Tertiary marine sedimentary deposits in the eastern part of the Crooked River subbasin. Several distinct hydrogeologic terranes have been defined in the Deschutes River Basin (Gonthier, 1985; Lite & Gannett, 2002). These include (a) pre-Tertiary marine deposits consisting predominantly of undifferentiated marine sediment, mudstone, shale, sandstone, and conglomerate; (b) deposits of the Eocene to Oligocene Clarno and John Day formations consisting of deeply weathered lava flows, vent deposits, volcanic breccias, volcanic sediment, and devitrified tuffs; (c) basalt flows of the Miocene Columbia River Group; (d) Pliocene volcanic sediment, pyroclastic materials, vent deposits, and lava, much of which is assigned to the Deschutes Formation; (e) quaternary deposits of the

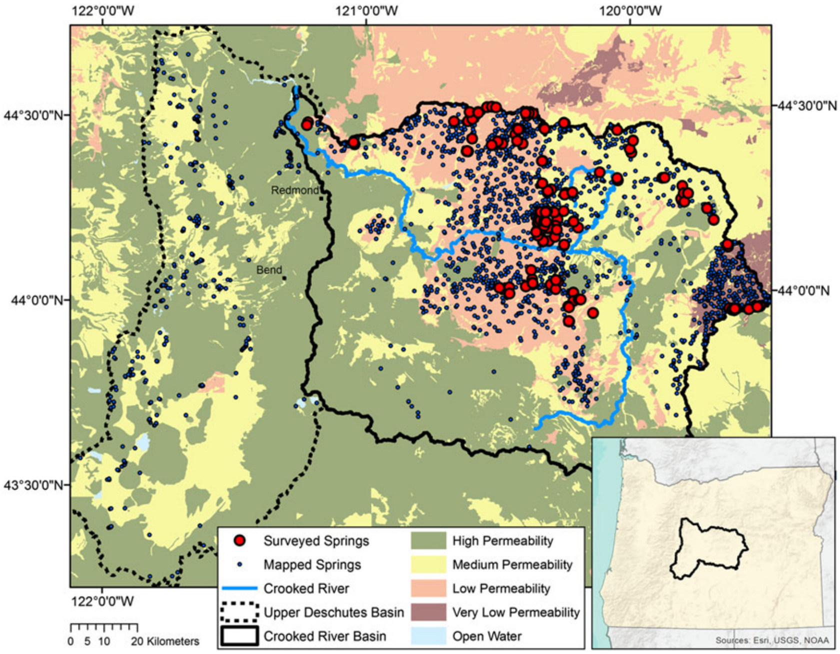

FIGURE 1 Mapped springs, visited springs, and geologic terranes in the Upper Deschutes River Basin, Oregon. Terranes are coloured by permeability category

Cascade Range and Newberry Volcano largely consisting of lava flows and domes, vent deposits, pyroclastic flows, and volcanic sediment; and (f) surficial alluvium, colluvium, and landslide deposits variously overlying the other units. These terranes generally reflect different ages, depositional processes, and primary lithologies (C. E. Brown & Thayer, 1966; Oregon Department of Geology and Mineral Industries, 2017; Sherrod et al., 2004; Swanson, 1969). Differences in the primary lithology, as well as age-related processes such as diagenesis, hydrothermal alteration, and secondary mineralization result in marked differences in hydrogeologic properties between different parts of the Deschutes Basin and Crooked River subbasin (Gonthier, 1985; Lite & Gannett, 2002).

2.2 | Permeability distribution

The permeability of the different geologic units within a basin can have a major influence on groundwater flow to springs, including the probable source areas, flow path lengths, and likely timescales of response to climate forcing. To investigate the hydrogeologic controls on spring distribution and characteristics, we classified each of the geologic terranes into permeability categories using a digital compilation of geologic mapping (Oregon Dept. of Geology and Mineral Industries, 2017) and previously defined hydrogeologic subdivisions (Gonthier, 1985; Lite & Gannett, 2002; Table 1, Figure 1). The permeability groupings were based primarily on geologic criteria such as primary lithology, and degree of secondary mineralization and weathering, combined with general assessments of groundwater conditions from the literature.

Although insufficient in number and distribution to be used alone to map the distribution of permeability, literature-derived hydraulic conductivity and transmissivity values can be used to illustrate the magnitude of differences in permeability between the independently defined map units (Table 1). Most of the literature sources (listed in Table 1) describe permeability (an intrinsic property of the medium) in terms of hydraulic conductivity (which includes the properties of the medium and the fluid). Some sources characterize aquifer permeability using transmissivity, which is the product of hydraulic conductivity and aquifer thickness.

Hydraulic conductivity differences among terranes in the Crooked River subbasin span several orders of magnitude (Table 1). The magnitude and range of hydraulic conductivity in an area are controlled by the primary lithology (which can be variable) and the age of the deposits. Primary lithology alone can cause geographic variations in hydraulic conductivity within a given terrane. Weathering, hydrothermal alteration, secondary mineralization, and diagenesis generally reduce the permeability of volcanic rocks with time (Freeze & Cherry, 1979). Secondary permeability resulting from faulting, fracturing, or dissolution can have a strong effect on groundwater flow in some settings (such as Karst regions), but permeability in the Deschutes Basin is more strongly controlled by original rock lithology and depositional processes (Gannett et al., 2001; Lite & Gannett, 2002). Although a range of hydraulic conductivity values have been estimated in each of the terranes, the upper and lower limits and average hydraulic conductivity differ among terranes and markedly decrease with increasing age.

2.3 | Landscape variables

Seven landscape-scale variables that describe the hydrogeologic and landscape settings of the springs and that may influence spring discharge type, discharge amount, and water chemistry were derived from other spatial datasets and summarized for each spring. These

TABLE 1 Permeability categories for terranes found in the Crooked and Upper Deschutes Basins and approximate ranges of average transmissivity and hydraulic conductivity estimates

Geology (terrane)	Range of transmissivity estimates ($m^2\ day^{-1}$)	Range of hydraulic conductivity estimates ($m\ day^{-1}$)	Permeability category	Sources
Pre-Tertiary igneous and metasedimentary rock	8–50	<0.003–0.3	Very Low	Gannett, 1984; Gonthier, 1985
Early Tertiary volcanic, volcaniclastic, and volcanic sediment deposits of the Clarno and John Day Formations	5–140	0.003–0.3	Low	Gannett, 1984; Gonthier, 1985
Basalt flows of the Miocene Columbia River Basalt Group	5–900	0.3–40	Medium	Ely et al., 2014; Gannett, 1984; Gonthier, 1985; Vaccaro et al., 2015
Quaternary surficial deposits	9–1,400	8–46	Medium	Gannett, 1984; Gonthier, 1985; Morgan, Hinkle, & Weick, 2007
Late Tertiary volcanic, volcaniclastic, and volcanic sediment deposits of the Deschutes Formation (and their age equivalents)	20–23,000	3–680	High	Gannett et al., 2001; Gannett, Lite, Risley, Pischel, & La Marche, 2017; Gonthier, 1985
Quaternary volcanic deposits of the Cascade Range and Newberry Volcano	50–74,000	1–300	High	Gannett et al., 2001, 2017; Gates & Gannett, 1996; Manga, 1997, Saar & Manga, 2004

Note. Transmissivity and hydraulic conductivity values were estimated in the cited sources using a variety of methods including analysis of specific capacity data from well logs, published aquifer tests, and model analysis.

were (a) catchment area (assuming no interbasin/intercatchment groundwater flow, except between catchments nested within each other), (b) precipitation at the spring, (c) elevation of the spring, (d) number of springs nested within a catchment, (e) number of springs in a spring complex (i.e., spring sites with multiple upwelling points found within the same wetland area; Junghans et al., 2016), (f) land cover type, and (g) spring density. Although surface catchment areas are not necessarily equivalent to recharge area for groundwater emerging at springs, they provide insight into the scale of probable contributing areas when considered in aggregate. Surface catchment areas were calculated using ArcHydro on a LiDAR-derived digital elevation model (USGS, 1999). In many cases, the catchment area of a spring encompasses one or more higher elevation springs. We calculated the number of higher elevation springs nested within a catchment area because water discharging from springs higher in the catchment may also serve as sources of recharge for lower elevation springs. Precipitation values are 30-year normals from 1981 to 2010 (PRISM Climate Group, 2017). Spring density was calculated in two ways. Each spring was evaluated for its proximity to other springs by calculating the mean distance to nearest neighbour for the nearest 10 springs within the same permeability category. Overall spring density for each permeability category also was calculated. Land cover represents the existing vegetation types found in the Crooked River subbasin (Table 2; LANDFIRE, 2008).

TABLE 2 LANDFIRE vegetation types used for analyses (LANDFIRE, 2008)

LANDFIRE vegetation types in the Crooked River subbasin, OR
1. Ponderosa Pine Forests and Woodlands
2. Mixed Conifer Forests
3. Alpine and Subalpine Habitats
4. Low, Black, and Rigid Sagebrush Steppe
5. Recently Burned Forest
6. Interior Lowland and Foothill Riparian Woods
7. Juniper Woodlands and Savannah
8. Montane Riparian Forests and Shrublands
9. Big Sagebrush Shrublands and Steppe
10. Columbia Basin Grasslands and Prairie
11. Aspen Forests and Woodlands

2.4 | Field inventories

Inventoried springs were located on public lands including the Ochoco National Forest and land managed by the Bureau of Land Management, as well as private land including The Nature Conservancy's Juniper Hills Preserve (Figure 2). All springs inventoried are in the run-off-dominated part of the Crooked River subbasin above the reach of the river with large regional groundwater discharge. Springs and spring complexes were selected initially from a stratified random sampling of mapped springs based on geology, ecoregion, and elevation. Additional sites were inventoried opportunistically, including both mapped and unmapped springs that were found during the surveys. Between July 2013 and October 2015, 137 springs or spring complexes were visited in the Crooked River subbasin (5.4% of mapped springs). Of the springs visited, 95 springs or spring complexes were found with flowing water. The remaining 42 mapped springs were ephemeral, extinct, or were artefacts of mapping error and were excluded from the spring inventory analyses. Springs were characterized by spring discharge type, temperature, specific conductivity, pH, discharge, and degree of disturbance or alteration.

- Spring discharge type was characterized as either discrete (defined as having a single concentrated point of groundwater discharge) or diffuse (defined as having multiple smaller point of groundwater discharge that often coalesce into channels downslope). Using the spring classification method of Springer and

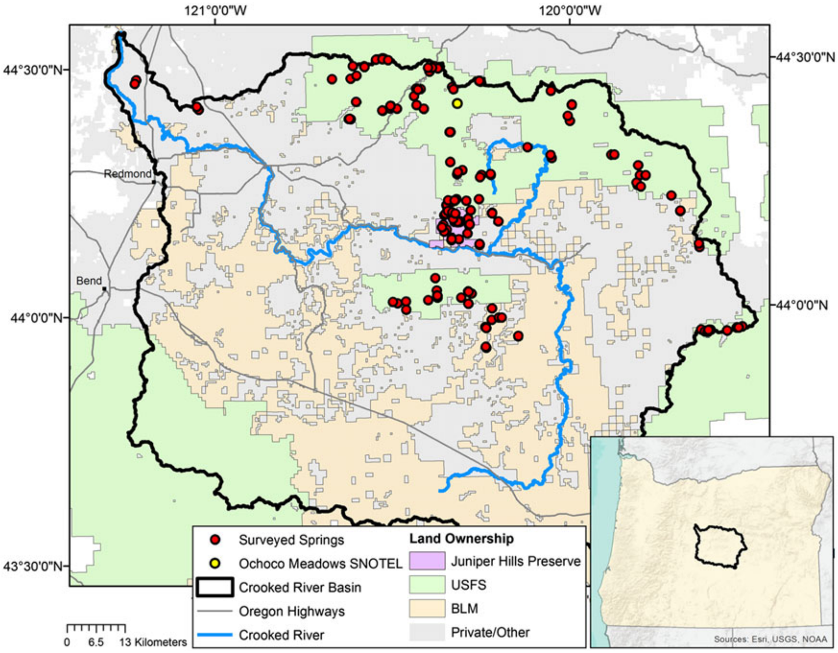

FIGURE 2 Surveyed springs, the Ochoco Meadows SNOTEL site, and land ownership in the Crooked River subbasin

Stevens (2009), the observed diffuse-discharge springs in the Crooked River subbasin included hillslope, helocrene, limnocrene, and fen springs. We do not attempt to distinguish among the four types in our analysis. The discrete-discharge type springs in the Crooked River subbasin are considered rheocrene (Springer & Stevens, 2009).

- Temperature, specific conductivity, and pH were measured using a calibrated YSI Pro-1030 meter. Measurements were made at the spring orifice to ensure that the conditions were representative of the groundwater and to minimize influence of insolation, vegetation, and other disturbances of the water chemistry parameters. Water quality measurements were made at 55 of the 95 visited springs. At the other 40 sites, either water chemistry was not measured, or data collected were later determined not to meet quality control standards and were discarded. Water quality data were not used if confounding factors were likely to affect the measurements. For example, it was often difficult or impossible to locate a specific groundwater upwelling point in diffuse-discharge springs, and some discrete-discharge springs had inaccessible orifices. Application of isotopic methods to determine whether the flow systems were local or regional was not practical for this study because stable isotope systematics have not been established in the Crooked River subbasin.
- Spring morphology and development dictated the method used to measure discharge. For developed springs at which all flow was diverted through a pipe, discharge was measured volumetrically using a timer and graduated cylinder (averaged among five trials). For undeveloped springs that coalesced into a channel, discharge was measured using a v-notch weir or flume (60° trapezoidal flume; Whitney Equipment Company, Inc.) located as close to the orifice as practical. The weir or flume was placed directly in the channel, and water was channelled through the instrument using native materials or plumber's putty. Discharge measurements were made at 43 of 95 visited springs. At the other sites, the discharge was too diffuse to measure or was below the detection limits of the weir or flumes.
- Each spring was evaluated qualitatively for whether its ecological or hydrologic function was significantly affected by the following types of disturbance: engineered spring developments and water diversions, livestock use, soil trampling/compaction, recreational use, and grazed vegetation.

The field inventories were done between May and October of each year due to lack of access to high-elevation springs during the winter months. Although interyear and intrayear climate variations could have an impact on measured spring chemistry and discharge, the large number of springs visited required a multiyear effort. Ninety percent of the inventoried springs were visited in 2014 or 2015, which had very similar water year precipitation totals of 549 and 579 mm, respectively, at the Ochoco Meadows SNOTEL site (Figure 2; Natural Resources Conservation Service, 2017).

Inventoried springs occasionally were found to be spring complexes with multiple discharge orifices. In these cases, field inventory measurements from different upwelling points are either summed (discharge) or averaged (pH, temperature, and specific conductivity). Although most springs and spring complexes were visited only once, 14 were visited multiple times (Appendix A). Measurements from springs with multiple visits were averaged. Although seasonal variation may have an impact on the repeated measurements at springs with multiple visits, there was an insufficient sample size to account for seasonality. Additionally, because all springs were visited after peak run-off and prior to the winter storm season, the effects of seasonal flow variations are assumed to be negligible. For the 14 spring complexes with multiple visits, there were no systematic changes in discharge or water chemistry among visits (Appendix B).

In addition to the spring inventory detailed above, 10 discrete-discharge springs were sampled for plant and macroinvertebrate richness and abundance in 2014 and 2016 (Appendix A). The 10 sites selected were those with the least disturbance from livestock, do not have engineered spring developments, were accessible for field crews, and were on public land. Relatively undisturbed sites were selected to develop an inventory of species that could colonize other springs in the basin because there have been no other inventories of spring flora or fauna in this region. Timing of these surveys was intended to maximize the ability to collect larval macroinvertebrates and ensure plants were in flower or had set seed. Macroinvertebrate sampling used techniques similar to those recommended in Sada and Pohlmann (2006). Macroinvertebrates were sampled from the spring orifice and up to 30 m of adjacent spring brook immediately downstream. All available microhabitats within the spring orifice and outflow areas were sampled, including the benthos; clumps of mosses and algae; submerged, emergent, and floating vegetation; and submerged branches and roots. When possible, samples were taken using standard D-frame aquatic nets with 500-μm Nitex mesh and a 1-ft^2 opening. When there was insufficient flow for D-frame sampling, mini-Surber nets or Petite Dip Nets were used (both 500-μm Nitex mesh). Species were identified to the lowest practical taxonomic level. Vegetation was surveyed by extending a line along the thalweg from the spring orifice downstream for 50 m. At 2-m intervals starting at the orifice, a cross line was extended across the spring brook perpendicular to the thalweg line. A 0.5 m × 0.5 m quadrat was placed with the upper right corner at a random point along the cross line and the upper end of the frame along the cross line. Species presence/absence was recorded in every quadrat, including both bryophytes and vascular plants, for a total of 25 plots per spring.

3 | DATA ANALYSIS

3.1 | Spring density and type

We used one-way ANCOVA to test the effects of the categorical predictor permeability and continuous covariate precipitation on spring density across the Crooked and Upper Deschutes subbasins (PROC GLM; SAS Institute, 2012). Differences among permeability categories were determined with post hoc pairwise tests using the Tukey–Kramer multiple comparison method. Spring density was $\log_{10}$ transformed to account for assumptions of normality and homogeneity of variances.

For this and all subsequent analyses, significance was evaluated at a threshold of $P < 0.05$.

We used logistic regression (PROC Logistic; SAS Institute, 2012) to test whether spring discharge type was associated with permeability, precipitation, elevation, catchment area, number of springs nested within a catchment, number of springs in a spring complex, and land cover type. Due to the large number of potential explanatory variables, a stepwise logistic regression (PROC Logistic; SAS Institute, 2012) was used to identify likely prognostic variables ($P < 0.30$ for entry; $P > 0.35$ for ejection) to include in the logistic regression model. Based on the outcome of the stepwise logistic regression, the final logistic regression model tested the association between discharge type and permeability, elevation, number of springs nested within a catchment, and number of springs in a spring complex.

3.2 | Habitat characteristics

Two-way ANCOVAs were used to test the relationships between spring physicochemical characteristics (discharge, temperature, pH, and specific conductivity) and spring discharge type, permeability, precipitation, catchment size, number of springs nested within a catchment, number of springs in a spring complex, and land cover. Both main effects and interaction terms were included in the ANCOVAs. Spring discharge type was included as an independent variable for the remainder of the analyses on spring physicochemical characteristics because these characteristics may vary based on spring discharge type. Pearson correlation analyses were used to determine covariance between each physicochemical characteristic and the continuous independent variables. Tukey–Kramer multiple comparison tests were done for post hoc pairwise comparisons between categorical variables.

3.3 | Biodiversity

Two measures of biodiversity were calculated from the vegetation and macroinvertebrate data collected at 10 discrete-discharge springs: (a) species richness (or total number of taxa found) and (b) relative species diversity measured using Shannon's index (Shannon & Weaver, 1949):

$$H' = -\sum_i^s p_i \log p_i,$$

where p_i is the relative proportion of species i and s is the number of species.

Multivariate multiple regressions were used to test associations between diversity (species richness and Shannon's index for both macroinvertebrates and vegetation) and physicochemical characteristics (discharge, temperature, pH, and specific conductivity). Because only discrete-discharge springs were surveyed for vegetation and macroinvertebrate community composition, we were unable to test the association between diversity and discharge type.

4 | RESULTS

4.1 | Spring density and type

The density of mapped springs in the Crooked and Upper Deschutes subbasins was significantly affected by permeability ($P < 0.0001$) and precipitation ($P < 0.0001$). Lowest mean distance to nearest 10 neighbours (i.e., greater spring density) was found in areas with higher precipitation among all permeability categories. Spring density was inversely related to permeability, with the lowest spring density in the "High" permeability terranes and the highest spring density in the "Very Low" permeability terranes (Figure 3). The distribution of springs within the permeability groupings appears to be largely controlled by topography, stratigraphy within units, and contacts between units (often with associated landslides). Some springs are associated with mapped faults in the Columbia River Basalt and on the margins of the Cascade Range.

The discharge type of a spring was related to spring elevation ($P = 0.017$) and number of springs in a complex ($P = 0.031$). Diffuse-discharge springs are more likely to be found at higher elevations and with more springs in the complex than discrete-discharge springs (Figure 4).

4.2 | Habitat characteristics

There were no significant main effects of terrane permeability on discharge, specific conductivity, temperature, or pH (Table 3).

Spring discharge was not significantly affected by any explanatory variable. Mean measured discharge ranged from 0.001 to 2.00 L s^{-1} but was below 0.10 L s^{-1} at 22 of the 43 sites with discharge measurements (Figure 5).

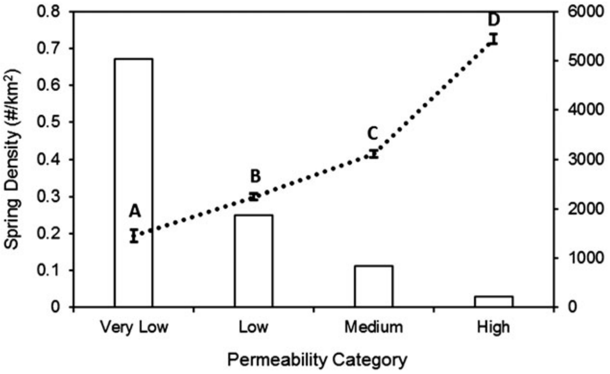

FIGURE 3 Effects of permeability category on spring density and mean distance to nearest 10 neighbours. Spring density is on the primary (left) y-axis, whereas mean distance to nearest 10 neighbours is on the secondary (right) y-axis. Spring density (represented by columns) was calculated for each permeability category, whereas mean distance to nearest 10 neighbours (represented by dashed line) is calculated for each spring. Mean distance values are ±*SE*. Significant pairwise comparisons are indicated by different letters above standard error bars

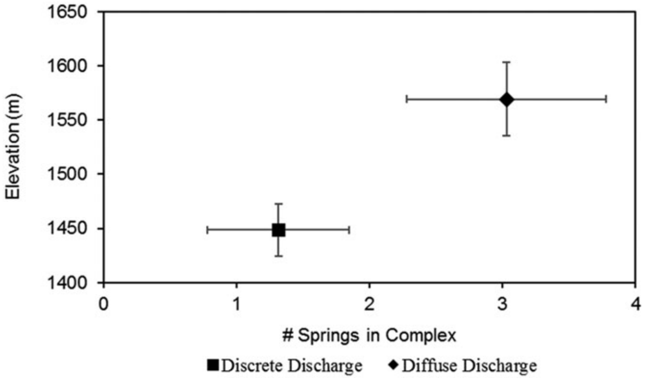

FIGURE 4 Bivariate plot of elevation and number of springs in a complex showing the difference between mean values for discrete-discharge springs (n = 66; square) and diffuse-discharge springs (n = 29; diamond). Values are means ± *SE*

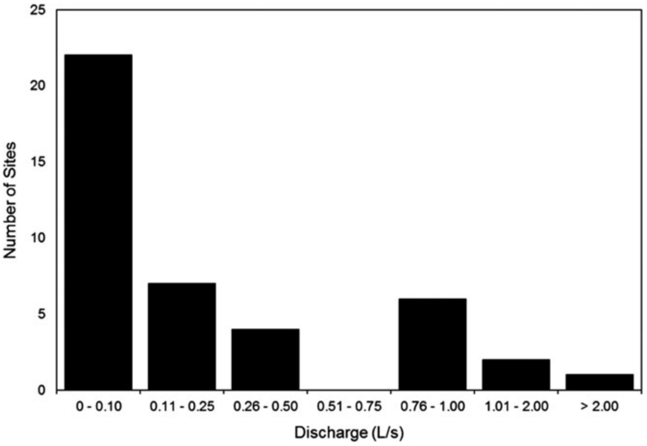

FIGURE 5 Histogram of discharge for the 43 springs or spring complexes with discharge measurements

Specific conductivity was significantly correlated to the number of springs nested in the catchment (P = 0.049; R^2 = 0.078), with greater specific conductivity correlated to more springs nested within the catchment.

Spring temperature was lower at higher elevations (P = 0.011; R^2 = 0.413), higher in diffuse-discharge type springs (P = 0.026), and significantly affected by the Permeability category × Discharge type interaction (P = 0.037). The interaction effect indicates that in discrete-discharge springs, temperature was generally higher among springs emerging in higher permeability terranes. In contrast, temperature in diffuse-discharge springs was highest among springs emerging in the low-permeability terrane category.

Land cover (P = 0.026), the Spring discharge type × Land cover interaction (P = 0.004), and the Spring discharge type × Permeability category interaction (P = 0.003) all significantly affected pH. Post hoc pairwise comparison tests show that pH was significantly lower in mixed conifer forests than in either juniper woodlands/savannah or big sagebrush shrublands and steppe. The interaction effect of Discharge type × Permeability category indicates that the pH of discrete-discharge springs was lowest in medium permeability category, whereas the pH of diffuse-discharge springs was lowest in the low-permeability category. The cause of the Discharge type ×Land cover interaction is obfuscated by the low sample sizes at this scale of division; among the 22 levels of the combined factors, n > 5 for only three levels.

4.3 | Field observations of disturbance and biodiversity

Developments for livestock watering, such as troughs, pipes, and spring boxes, were found in 43% of the springs surveyed. Undeveloped springs commonly had evidence of livestock alteration and disturbance. Of the springs surveyed, 95% of diffuse and 79% of discrete springs were affected by livestock in some way (Appendix C). The most common evidence of livestock alteration was soil trampling, followed by browsed vegetation at the spring orifice and cow faeces observed in or adjacent to the spring. Eight springs did not have enough information to determine evidence of livestock alteration, or observations were not recorded.

One hundred thirty-five unique macroinvertebrate taxa were found among the 10 discrete-discharge springs. There were no statistically significant relationships between the physicochemical characteristics and macroinvertebrate richness or Shannon's index of diversity (H'). Shannon's index for the macroinvertebrates at the 10 sampled sites ranged from 1.6 to 2.9 with a mean of 2.1. The greatest diversity occurred among the Diptera, which were represented by members of 13 families. The greatest total abundance was contributed by *Pristinicola hemphilli* (Pristine Pyrg), a snail associated with cold water and spring habitats. A mixture of lotic, lentic, and marginal taxa was found in the wide variety of microhabitats sampled in each spring. Because these are the only perennially wet habitats throughout most of the Crooked River subbasin, the springs contribute substantially

TABLE 3 Means and range of physicochemical characteristics of springs by terrane permeability rank

Terrane permeability rank	No. of Springs with physicochemical data	Discharge (L s^{-1}); mean (range)	pH (standard units); mean (range)	Temperature (°C); mean (range)	Specific conductance (µS cm^{-1} @ 25°C); mean (range)
Very Low	3	0.217 (0.013–0.421)	7.17 (7.13–7.22)	9.98 (9.0–10.9)	368.1 (323.0–413.2)
Low	53	0.264 (0.002–1.55)	6.91 (5.81–8.67)	11.53 (6.2–19.5)	245.6 (30.0–704.1)
Medium	32	0.387 (0.001–2.01)	6.86 (6.21–7.31)	8.74 (5.0–18.4)	197.9 (53.8–461.5)
High	7	0.270 (0.047–0.783)	7.00 (6.90–7.33)	11.2 (8.0–14.1)	346.9 (131.1–704.0)

Note. There were no significant differences of physicochemical characteristics among terrane permeability ranks. The number of springs with physicochemical data represents springs with at least one measurement of at least one data type. Many springs did not have discharge measurements when discharge was too diffuse to measure with a weir or flume, or when discharge was below the detection limits.

to the overall biodiversity of the area. The most noticeable taxa missing from the Crooked Basin springs were the Odonata (dragonflies and damselflies). At least four damselfly taxa were found among the Oregon springs surveyed by Anderson and Anderson (1995), and other studies of western springs have also found multiple species of odonates (Myers & Resh, 2002; Rudisill & Bass, 2005; Stagliano, 2008; Weissinger, Perkins, & Dinger, 2012).

One hundred fifty-one species of plants were identified from the 10 spring sites, of which 66 species are wetland-dependent (i.e., ranked "obligate" or "facultative wet"; U.S. Army Corps of Engineers, 2012). Shannon's index (H') for the vegetation at the 10 sampled sites ranged from 1.9 to 2.8 with a mean of 2.4. Plant richness and H' were both inversely correlated to spring discharge ($P = 0.044$; Figure 6). No other associations between diversity and physicochemical characteristics were statistically significant. No plants or macroinvertebrates identified in these surveys were on the Endangered Species List.

5 | DISCUSSION

Despite their importance for local livestock economies and ecosystems, low-discharge springs are poorly studied in comparison with their higher discharge counterparts. There are no other studies of small springs systems in Oregon, compared with numerous publications describing larger springs and their supporting aquifer systems (Gannett et al., 2001, 2003; Gannett, Lite, La Marche, Fisher, & Polette, 2007; James et al., 2000; Manga, 1996, 1997, 1999, 2001; Meinzer, 1927; Whiting & Moog, 2001). Even studies of large, regional spring systems commonly do not describe the species supported by them. This study provides evidence that the hydrogeologic setting is a strong driver of the distribution of springs across the landscape and the characteristics of the spring habitats.

Both precipitation amount and bedrock permeability affect spring density. Springs are more densely distributed across low-permeability terranes, such as pre-Tertiary marine deposits, and are comparatively sparse in high-permeability terranes like the young Quaternary deposits of the Cascade Range (Figures 1 and 3). We propose that the inverse relationship between permeability and spring density is due to the limited infiltration of rain and snowmelt in low-permeability terranes and concentration of flow in the soil zone and shallow bedrock. Such terranes generally lack sufficient through-going interconnected zones of permeability at depth for regional-scale aquifer systems to exist. In low-permeability terrane, a large proportion of groundwater is restricted to shallow, short flow paths that easily intersect the land surface, resulting in many springs.

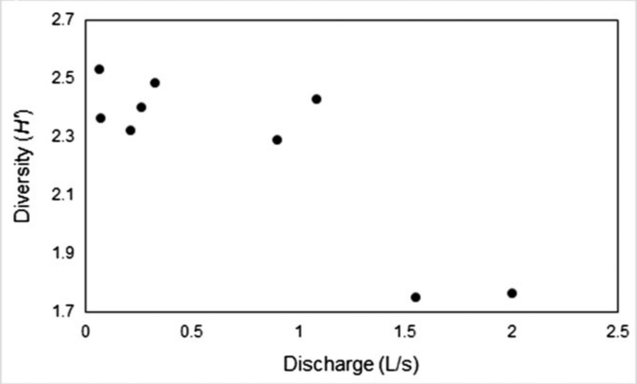

FIGURE 6 Relationship between Shannon's index of diversity (H'; Shannon & Weaver, 1949) for plants and measured discharge at nine of the 10 sites with vegetation surveys. The remaining site with vegetation data does not have a discharge measurement because the spring outflow did not coalesce into a well-defined spring brook

Water in these shallow flow paths may cycle into and out of the groundwater system multiple times as it is discharged from springs, flows on the land surface for a short distance, and infiltrates back into the soil. Many of the springs we inventoried flowed less than 50 m before the water re-infiltrated into the soil. In contrast, precipitation falling on higher permeability terranes such as Quaternary lava flows has been shown to infiltrate to deep regional aquifer systems more effectively, resulting in longer flow paths integrating larger recharge areas with fewer opportunities to discharge through springs at the land surface (Gannett et al., 2001; Manga, 1997). For example, temperature and isotope data collected from Opal Springs on the Crooked River about 11 km from its confluence with the Deschutes River indicate that the source is tens of kilometres away in the Cascade Range (James et al., 2000).

This conceptual model of permeability and spring density suggests that discharge should be higher and more consistent from springs found in high-permeability terrane than those found in low-permeability terrane, if all other variables are equal. Within the larger Deschutes Basin, this relation clearly exists. Springs and spring complexes with discharge rates ranging as large 700 to 6,800 L s^{-1} are documented in the high-permeability terrane in the Deschutes Basin, including the lowermost Crooked River canyon (Caldwell, 1998; James et al., 2000). No springs with similar large discharge are known in the low-permeability terranes of the Deschutes Basin, including the Crooked River subbasin. The mean discharge measured during this study in the low-permeability terrane was 0.264 L s^{-1} (±0.161 *SE*, $n = 18$). Surprisingly, discharge from springs in the high-permeability category terrane in the Crooked River subbasin measured for this study (0.270 L s^{-1}, ±0.151 *SE*, $n = 4$) was not significantly different. This highlights the influence of other factors on spring discharge, such as available precipitation and aquifer boundaries. Although large and potentially through-going permeability creates the potential for deep infiltration, long groundwater flow paths, large source areas for springs, and large discharge, these characteristics are also substantially influenced by climate and aquifer boundaries. The high-permeability areas from which large-discharge springs emerge in the western Deschutes Basin include the Cascade Range, where annual precipitation is as high as 4,200 mm $year^{-1}$ (Gannett et al., 2003). Moreover, the supporting aquifer systems have flow paths exceeding 50 km, allowing for integration of recharge over large areas (James et al., 2000; Gannett et al., 2001, 2003; Waibel et al., 2013). The high-permeability regions sampled in the Crooked River subbasin for this study, in contrast, are much more arid, with annual precipitation of less than 700 mm. In addition, the permeable regions in the area sampled for this study are generally isolated patches a few kilometres across, precluding large catchment areas across which recharge can be integrated. The relationship between bedrock permeability and spring density should be tested in other geographies and may inform water resource management in water-limited areas. For example, groundwater potential mapping (e.g., Naghibi & Dashtpagerdi, 2017) could incorporate bedrock permeability as a groundwater influence factor.

In addition to geology controlling the distribution of springs across the landscape, the spring habitat characteristics are also related to the hydrogeologic setting. Discharge type, measured discharge, specific conductivity, temperature, and pH were all affected by landscape variables, supporting the concept that landscape-scale analysis can be used to better understand likely site-scale characteristics. Diffuse springs were found more frequently at higher elevations throughout the study region than discrete springs but had higher mean temperature. This is inconsistent with the overall inverse relationship between temperature and elevation. However, diffuse springs had consistently higher temperatures than discrete springs at a given elevation. There are two likely explanations for this trend. First, many low-discharge diffuse springs had slow-moving or pooled water at the spring orifice. At the time of sampling, the pooled water had a higher temperature than the emerging groundwater due to insolation, and the water in the spring orifice may have mixed well enough to allow the pooled water to influence the temperature measurement. Second, it is possible that some low-discharge diffuse springs had very shallow flow paths uphill of the orifice, which allowed heat exchange between the groundwater and the warmer soil subsurface (Alkhaier, Schotting, & Su, 2009).

The pH measured in springs was lowest, and closest to the pH of precipitation, in the mixed conifer habitat type compared with other habitat types. The lower pH may indicate that water in the mixed conifer habitat is discharging from shorter flow paths from the recharge areas and thus has chemical characteristics more closely approximating precipitation. Mixed conifer habitat is generally found in higher elevations throughout the Crooked River subbasin. However, pH was not significantly related to either elevation or catchment size in the two-way ANCOVA model. The lower pH in mixed conifer forests may also be due to shallow groundwater flow paths contacting more acidic soils that are generally found in coniferous forests (Berthrong, Jobbagy, & Jackson, 2009). Within the coniferous forests, the diffuse-discharge springs had lower pH (mean = 6.23, ±0.95 *SE*, *n* = 9) compared with the discrete-discharge springs (mean = 6.70, ±0.10 *SE*, *n* = 8), possibly due to greater contact of the diffuse-discharge pathways with the forest soils. Alternatively, longer residence times of water within the spring orifice of diffuse-discharge springs may allow for conifer needle leachate to affect pH measurements.

Despite widespread disturbance and alteration, the macroinvertebrate and vegetation surveys confirm that springs are islands of biodiversity in the central Oregon landscape, with 134 macroinvertebrate taxa and 151 plant species found associated with spring habitats. This is consistent with other studies (e.g., Shepard, 1993). The macroinvertebrate species richness is similar to that found in other studies of western springs (Myers & Resh, 2002; Rudisill & Bass, 2005) and higher than the only other study of aquatic invertebrates done specifically in central Oregon springs (Anderson & Anderson, 1995). The vegetation surveys showed that nearly half of the 151 plant species identified are wetland-dependent and many of these require perennial water. In this landscape, perennial water is only supplied by springs because most streams at higher elevation are ephemeral or intermittent. For comparison, studies of dry pine forests, which is the major habitat type surrounding the springs, have total species richness often lower than 20 (Busse, Simon, & Riegel, 2000; Metlen & Fiedler, 2006; Thomas, Halpern, Falk, Liguori, & Austin, 1999). We were not able to identify any comprehensive vegetation surveys from spring habitats in similar climates. Although vegetation was only surveyed in discrete springs in this study, diffuse springs support different types of plant communities than discrete springs (e.g., Springer et al., 2015). In addition to the high species richness documented, most of the springs were located uphill from large mesic meadows, suggesting that discharge from these springs also supports these habitats that offer forage for wildlife and livestock alike.

Given the importance of the hydrogeologic setting as a primary control of the distribution of species in groundwater-dependent ecosystems (Bedford & Godwin, 2003; Godwin et al., 2002), we expected to see relationships between physicochemical characteristics and measures of diversity. We only observed an inverse correlation between spring discharge and vegetation richness and diversity, which is driven primarily by two outlier springs with relatively high discharge and relatively low plant richness and diversity (Figure 6). Although interpretation of this analysis is limited by the small sample size, there may be an ecological explanation for this relationship. The greater erosive potential of high-discharge springs could limit the amount of spring brook microhabitats by confining the water to a well-defined channel. In contrast, low-discharge springs—many of which coalesce to form a shallow, poorly defined channel—could create conditions for more microhabitats, such as pools or larger wetted riparian areas. However, a more comprehensive survey of spring flora is needed to determine if this relationship remains true with greater statistical power.

There were no odonates (dragonflies and damselflies) found during the macroinvertebrate surveys. The only other study of aquatic macroinvertebrates in central Oregon springs—in which odonates were found—surveyed diffuse springs (Anderson & Anderson, 1995), whereas the springs surveyed for diversity and richness in this study were all discrete-discharge. Although other factors may account for the different results in the two surveys, this finding is consistent with other studies that show that odonates are rarer in lotic waterbodies than lentic ones (Balzan, 2012; Korkeamaki & Suhonen, 2002; White & Switzer, 2013). Odonates also are sensitive to disturbance and degradation of environmental conditions and are considered excellent indicator species (Clark & Samways, 1996). Although both this study and Anderson and Anderson (1995) attempted to survey springs with minimal disturbance, those surveyed in this study may have been degraded beyond the ability to support odonate larvae. Evidence of nearby livestock grazing was found near all 10 surveyed springs, so although they were among the least disturbed of those we surveyed, they are not pristine.

The majority of springs—of both discharge types, at all elevations, and regardless of land ownership—were ecologically impaired in some way by livestock use. The extent of spring disturbance found in this study was considerably higher than other published surveys of spring disturbance in the semiarid or arid West (e.g., Sada et al., 1992; Sada et al., 2005). Livestock grazing is one of the most common uses of public land in the western United States. In these semiarid landscapes, the most reliable source of water is from springs, and land management agencies offer best management practices for spring development for livestock water supply (e.g., Natural Resources Conservation Service, 2013; USDA Forest Service, 2012a, 2012b). Those agency guidelines do not offer specific designs that protect the plants and animals that live in the springs, despite acknowledging the necessity of protecting spring ecosystems. This may be due to an absence of information about groundwater-dependent species and ecological values of these habitats, or it might be because small springs such as these are not protected under state or federal law. Additionally, the emphasis among land and water managers for the last several decades has been to protect rivers and riparian habitats. Springs are often off-channel and isolated, so small springs may receive lower priority compared with the larger objective of protecting the water and water quality of connected river networks.

Many of the springs visited during the inventory in the Crooked River subbasin were unmapped and were opportunistically sampled while travelling to the mapped springs that were preselected for the study. The high number of unmapped springs emphasizes the need for additional surveys to better understand the actual distribution of springs in the region. Ultimately, more surveys in the Crooked River subbasin or the Deschutes Basin could provide the data needed to utilize accumulation curves to estimate actual spring density (Junghans et al., 2016). Management actions such as monitoring and spring restoration efforts would benefit from an improved understanding of the number and distribution of springs, including the likely numerous unmapped springs (Junghans et al., 2016).

The relationship between geology and spring discharge has important implications for the springs' relative vulnerabilities to various hydrologic stressors. Low-discharge springs with local, shallow flow paths and smaller aquifer volumes are more likely to be rapidly affected by groundwater extraction and climate stresses such as drought and higher air temperatures, in contrast to longer flow-path regional springs (Aldous, Gannett, Keith, & O'Connor, 2015; Manga, 1999; Waibel et al., 2013).

Global climate models, meteorological data, and snow models predict climate warming in the Pacific Northwest and a shift in the form of winter precipitation from snow to rain at high elevations (Knowles, Dettinger, & Cayan, 2006; Mote & Salathé, 2010; Nolin & Daly, 2006; Sproles, Nolin, Rittger, & Painter, 2013). Shifts in the timing of run-off in snow-driven watersheds attributed to warming have been observed in the western United States (Cayan, Kammerdiener, Dettinger, Caprio, & Peterson, 2001; Chang, Jung, Steele, & Gannett, 2012; Jefferson, 2011; Mayer & Naman, 2011; Stewart, Cayan, & Dettinger, 2004). These changes in snow hydrology are expected to result in declines of high-elevation groundwater recharge (Meixner et al., 2016) and/or a shift in the timing of recharge to earlier in the water year (Tague & Grant, 2009; Waibel et al., 2013). Although the effects of shifts in timing of recharge may be moderated by aquifer storage in systems with large volume or long flow paths (Tague & Grant, 2009; Tague, Grant, Farrell, Choate, & Jefferson, 2008; Waibel et al., 2013), springs supplied by systems with shallow or short flow paths, such as those found in low-permeability terranes, will experience more marked reductions in late-season flow and increased incidents of seasonal drying.

In addition to the direct stressors of climate change, a probable increase in the frequency and extent of summer drought in the Pacific Northwest (Ahmadalipour, Moradkhani, & Svoboda, 2016) may lead to increasing demand for shallow groundwater to support livestock and increases in evapotranspiration rates from spring habitats. These forecasted decreases in supply and increases in demand could have a lasting impact on the many species dependent upon these small low-discharge springs.

More research on spring ecohydrology needs to be done to develop a rigorous understanding of these sensitive systems. Peer-reviewed literature on semiarid spring flora and fauna is extremely limited. Future biological inventories should follow a standardized methodology for comparability across geographies, and inventories should be done across a range of spring types. Better information of the biota supported by springs will strengthen efforts to understand the ecological needs of spring communities, which is necessary for better spring management. Long-term continuous monitoring of spring discharge and physicochemical characteristics is vital to developing a more rigorous understanding of the relationships among geology, climate, and spring discharge. More research is particularly needed to understand how springs—especially small springs—respond to annual and decadal oscillations in precipitation and temperature. Finally, additional studies are needed to determine if the inverse relationship between bedrock permeability and spring density is consistent in other geologic provinces. In the meantime, better local protection of springs where they are used as water supplies for people or livestock would help protect these diverse systems.

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APPENDIX A

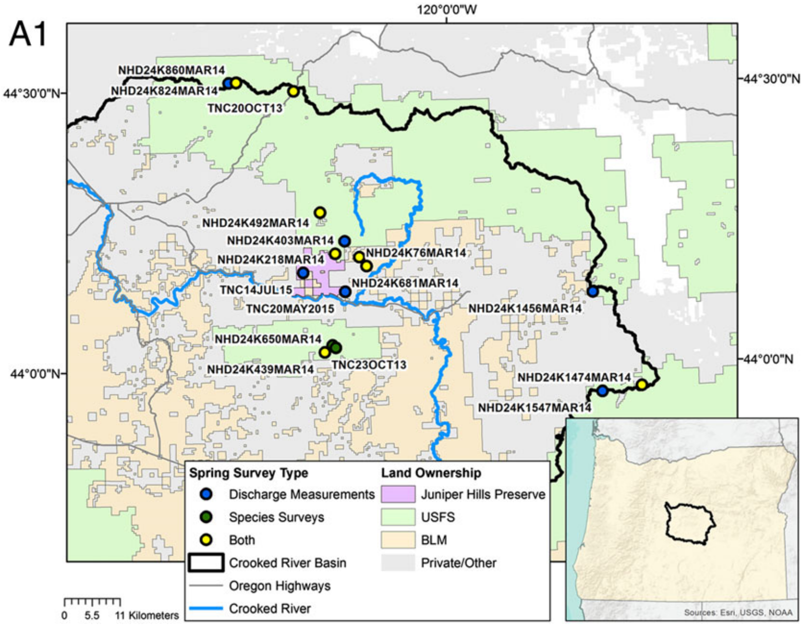

FIGURE A1 Location of springs with macroinvertebrate and vegetation species surveys (green dots), springs with multiple discharge measurements over time (blue dots), and springs with both species surveys and multiple discharge measurements over time (yellow dots)

APPENDIX B

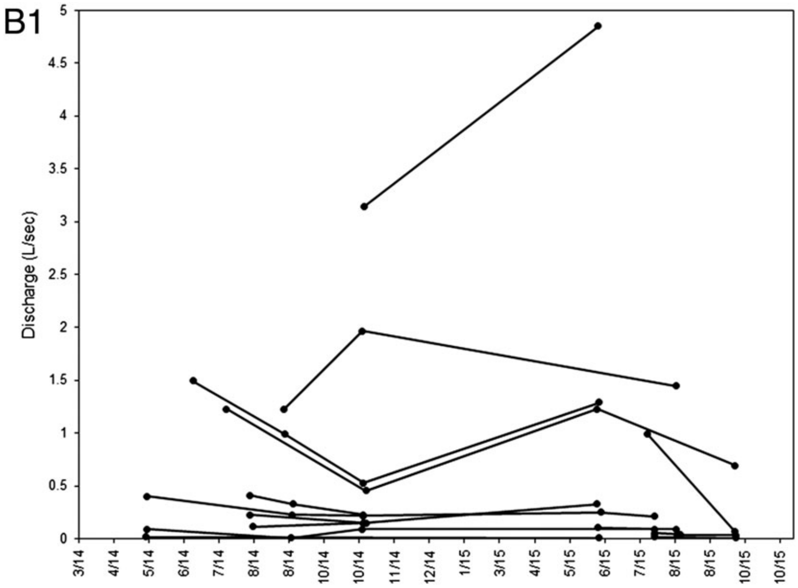

FIGURE B1 Change in discharge measurements over time for the 14 spring complexes with multiple site visits. Springs with multiple measurements include Horse Spring (NHD24K403MAR14), Warm Spring (NHD24K1547MAR14), Brooke's Spring (TNC20MAY2015), North Fork WSA Spring (NHD24K681MAR14), Sand Spring (NHD24K218MAR14), USFS Telephone Spring (NHD24K1456MAR14), Timothy Spring (NHD24K1477MAR14), Trail Meadow Spring (NHD24K824MAR14), Two Tree Spring (TNC14JUL15), Bingham Spring (NHD24K860MAR14), Double Cabin Spring (NHD24K439MAR14), Grays Prairie (NHD24K492MAR14), Ochoco Divide Spring (TNC20OCT13), and BLM Telephone Spring (NHD24K388MAR14)

APPENDIX C

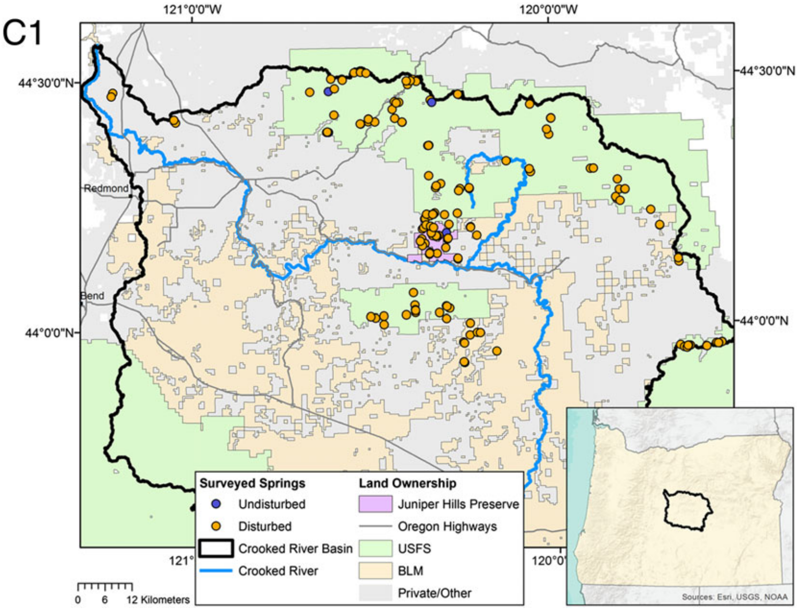

FIGURE C1 Location of springs with and without evidence of livestock disturbance overlaying land ownership in the Crooked River subbasin