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Streamflow permanence in headwater streams across four geomorphic provinces in Northern California

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Abstract

Mountainous headwater streams represent a substantial proportion of the global stream network. These small streams may flow episodically, seasonally, or perennially, providing diverse values and services. Given their broad importance and growing pressures on terrestrial and aquatic resources, we must improve our understanding of the drivers of flow permanence to facilitate informed land and water management decisions. We used field observations from >10 cross-sections in each of 101 non-fish bearing, headwater streams across four geomorphic provinces in Northern California to quantify flow permanence and network connectivity during the summer low flow period in 2018. At each stream cross-section, we noted the presence or absence of streamflow and used this information to classify streams as perennial (continuous streamflow in all cross-sections) or non-perennial and connected (surface water in the most downstream cross-section) or disconnected. At each cross-section, we also quantified channel size (width and depth) and grain size. We coupled field observations with geospatial data of catchment physiography, hydrology, and climate in random forest models to investigate controls of flow permanence and network connectivity. Potential drivers of flow permanence or network connectivity included in our models were channel geometry, grain size, slope, aspect, elevation, annual and seasonal precipitation, air temperature, and topographic wetness index. We found more perennial streams in the Klamath Mountains and Sierra Nevada than in the Cascades and N. Coast regions. Streams in the Klamath were the most connected followed by streams in the N. Coast, Sierra Nevada, and Cascades. The most important variables for predicting flow permanence were channel grain size, winter 2018 precipitation, and drainage area. Comparatively, the most important variables for predicting network connectivity were winter and spring 2018 precipitation, grain size, and bankfull depth. Our study illustrated the complexity of the processes that drive flow permanence and highlighted the uncertainty in projecting the precense of water in streams across diverse regions.

KEYWORDS
channel geometry, ephemeral streams, grain size, network connectivity, perennial streams, water supply

1 | INTRODUCTION

First order, forested headwater streams comprise ~50–80% of the cumulative length of the global stream network (Downing et al., 2012; Hansen, 2001; Nadeau & Rains, 2007). Despite their small size, forested source water streams are critical for the supply of water, sediment, nutrients, and organic matter to downstream water bodies (Peterson et al., 2001; Rodriguez-Cardona, Wymore, & McDowell, 2016; Wohl, 2017). In addition, forested headwater streams provide key habitat for fish and other aquatic organisms (Montgomery, 1999; Richardson & Danehy, 2007; Welsh & Hodgson, 2008; Wipfli, Richardson, & Naiman, 2007). Headwater streams also provide the primary source of water supply for domestic, agricultural, and industrial needs in many parts of the world (Brown, Hobbins, & Ramirez, 2008; Furniss et al., 2010; Robinne et al., 2019). Moreover, downstream water quantity, water quality, and aquatic habitat largely reflect the condition of upstream contributing headwaters (Alexander, Boyer, Smith, Schwarz, & Moore, 2007; Dodds & Oakes, 2008; Meyer et al., 2007). However, despite their exceptional importance, Bishop et al. (2008) noted the surprising lack of knowledge about headwater streams. While there has been a growing body of literature, which has improved knowledge on the abiotic properties, physical properties, and downstream scale of influence of headwater streams (Bladon, Segura, Cook, Bywater-Reyes, & Reiter, 2018; Costigan, Jaeger, Goss, Fritz, & Goebel, 2016; Janisch, Wondzell, & Ehinger, 2012; Raymond et al., 2013; Wohl, 2017), there are still numerous uncertainties, especially regarding the spatial and temporal dynamics of the streamflow regime in headwater catchments (Nadeau & Rains, 2007).

Many headwater streams are classified as ephemeral or intermittent and, as such, only supply water to downstream reaches during certain times of the year (Buttle et al., 2012; Datry, Fritz, & Leigh, 2016; Datry, Larned, & Tockner, 2014). Indeed, during low flow periods the flowing channel segments of temporary streams often alternate with dry channel segments, creating longitudinally discontinuous flow (Larned et al., 2011; Osterkamp, 2008; Reynolds, Shafroth, & Poff, 2015). However, in recent years, there have been rising concerns that the number and length of temporary streams may increase in many regions due to a warmer and dryer climate and greater demand for water resources (Acuna et al., 2014; Buttle et al., 2012; Larned, Datry, Arscott, & Tockner, 2010; Milliman, Farnsworth, Jones, Xu, & Smith, 2008). These mounting pressures could reduce streamflow in some regions, shifting many headwater perennial streams to intermittent or ephemeral streams (Winter, 2007). Declines in flow permanence and loss of connection to larger river systems pose substantial threats to both headwater and downstream aquatic ecosystem health (Levick et al., 2008; Tzoraki, Nikolaidis, Amaxidis, & Skoulikidis, 2007). Consequently, there is a need to improve our understanding of the spatial and temporal occurrence and drivers of flow permanence (Datry, Arscott, & Sabater, 2011).

Recent efforts have illustrated the utility of regional climatic data, combined with physical characteristics of forested headwater streams and catchments, for the determination of hydrologic permanence (Fritz, Johnson, & Walters, 2008; Jaeger et al., 2019). Not surprisingly, the research has shown that streamflow generation is highly variable in space and time due to complex interactions between precipitation and catchment physiographic characteristics, including land cover, soils, geology, and topography (Gutierrez-Jurado, Partington, Batelaan, Cook, & Shanafield, 2019; Mosley, 1979; Seyfried, Grant, Marks, Winstral, & McNamara, 2009; Winter, 2007). For example, Jaeger et al. (2019) developed a model to predict streamflow permanence for the Pacific Northwest Region, USA, and found that total annual precipitation and percent forest cover were consistently the most important predictors. However, they noted that important local-scale controls, such as surficial and hydrogeologic controls, were not adequately represented in their model (Jaeger et al., 2019). While others have also noted the importance of various precipitation metrics (e.g., annual precipitation, snow water equivalent, snowpack persistence) or percent forest cover as predictors of flow permanence (Reynolds et al., 2015; Sando & Blasch, 2015), additional indicators of flow permanence have included catchment area, bankfull width, bankfull ratio (i.e., ratio of bankfull width to bankfull depth), channel entrenchment or confinement, channel slope, soil type, bedrock permeability, and topographic wetness metrics (Costigan et al., 2016; Fritz et al., 2008; González-Ferreras & Barquín, 2017; Jaeger, Montgomery, & Bolton, 2007; Jencso & McGlynn, 2011).

Due to the high variability in the potential drivers of flow permanence, combined with the dynamic nature of regional hydrology, predictions of the spatial and temporal occurrence of streamflow permanence remain challenging. To improve model projections and capture the over-arching drivers of flow permanence, it is critical to consider field observations at regional scales, where possible (González-Ferreras & Barquín, 2017). Thus, the primary objectives of our study were to quantify flow permanence and network connectivity in non-fish bearing, headwater streams of four distinct geomorphic provinces in northern California during the summer low flow period in 2018. We also sought to quantify potential drivers of flow permanence and network connectivity, including channel geometry, grain size, slope, aspect, elevation, precipitation, and air temperature.

We found strong differences in the occurrence of perennial streams across the four study sub-regions. There were more perennial streams in the Klamath Mountains and Sierra Nevada than in the Southern Cascades and North Coast regions. Moreover, streams in the Klamath had higher downstream, network connectivity relative to the streams in the N. Coast, Sierra Nevada, and S. Cascades. Interestingly, the most important variables for predicting flow permanence were channel grain size, winter 2018 precipitation, and drainage area. In comparison, the most important variables for predicting network connectivity were winter and spring 2018 precipitation, grain size, and bankfull depth.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted a stratified field campaign in 25–26 non-fish bearing, headwater streams in each of four geomorphic provinces in California:

Northern Coast Range (N. Coast), Southern Cascade Range (S. Cascades), Klamath Mountains (Klamath), and Sierra Nevada Range (Sierra Nevada; Figure 1). These geomorphic provinces covered $\sim 2.3 \times 10^7$ ha of topographically diverse terrain and included geologic formations that vary in age (e.g., 1,000–2 Ma years), lithology, and dominant rock type (Table 1). Stream reaches located in the N. Coast

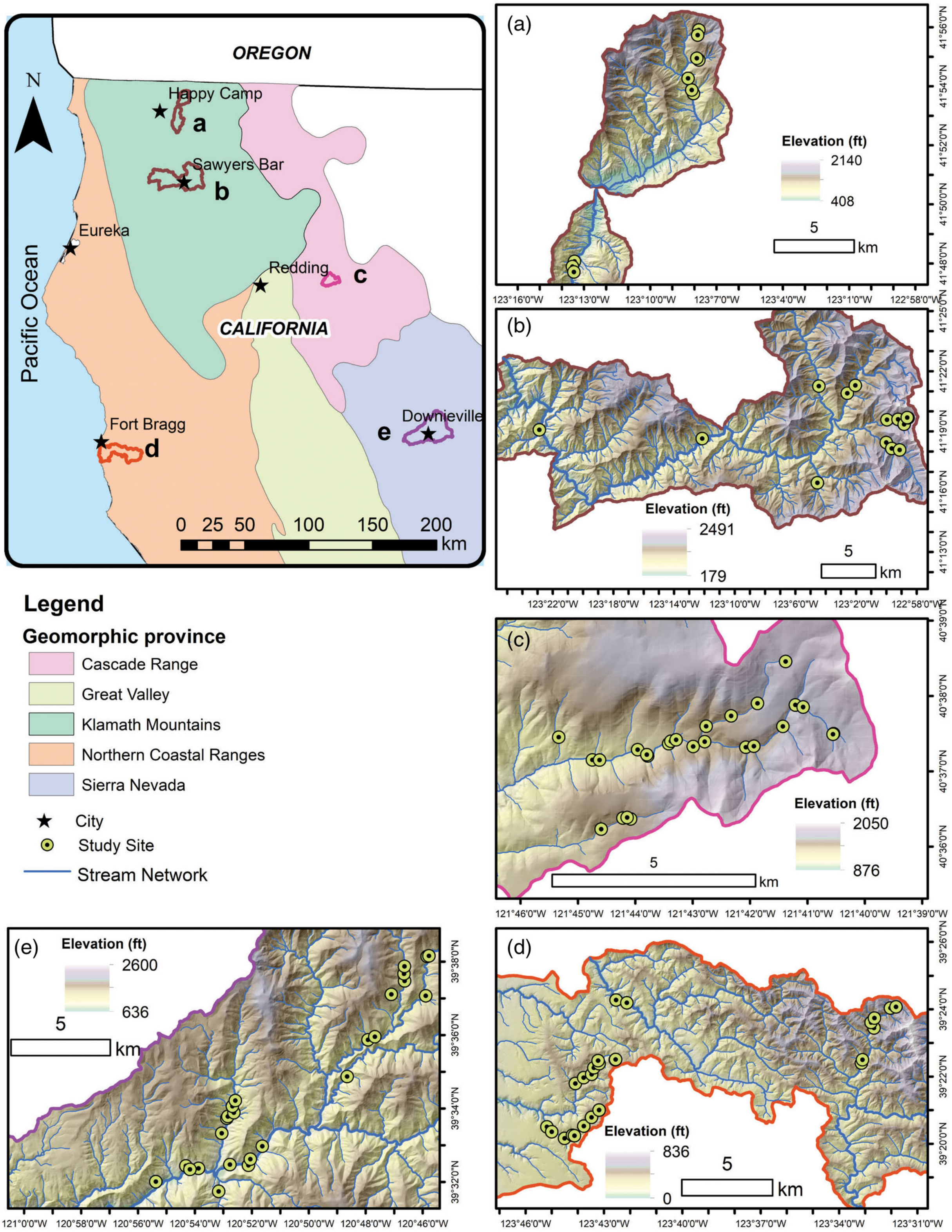

FIGURE 1 Maps of the general study area in California and site locations within each geomorphic province, including (a, b) Klamath Mountains, (c) Cascade Range, (d) Northern Coastal Range, and (e) Sierra Nevada

TABLE 1 Climate, elevation, lithology, and mean forest age in the four geomorphic provinces

	30-year Normal climate[a]		2018 water year climate[b]					Vegetation age[e]	
Geomorphic province	T_{air} (°C)	P (mm)	T_{air} (°C)	P (mm)	April first SWE (mm)[c]	Mean elevation (m)[d]	Lithology	(years)	# of sites
N. Coast	12.9 (0)	1,256.3 (22)	12.9 (0.3)	928.4 (23)	0	242 (80)	Sedimentary: sandstone, mudstone	87 (19)	25
S. Cascade	9.5 (1)	1,334.2 (22)	9.9 (0.8)	1,253.2 (62)	676	1,687 (138)	Igneous: andesite, basalt, rhyolite	99 (43)	26
Klamath Mountains	10.2 (2)	1,327.1 (212)	11.4 (1.4)	825.5 (225)	499–689	1,482 (454)	Mixed: diorite, argillite, greenschist, intermediate volcanic rock	129 (80)	25
Sierra-Nevada	11.8 (1)	1,650 (63)	12.4 (0.8)	1,654.6 (70)	961–963	1,318 (182)	Mixed: argillite, peridotite, intermediate volcanic rock	105 (45)	25

Note: Mean and standard deviation (in parentheses) were calculated across the sites investigates in each region.

[a] 30-year normal (1980–2010; PRISM Climate Group, 2004).

[b] 2018 water year (Thornton et al., 2018).

[c] Snow water equivalent (SWE; USDA Natural Resources Conservation Service, 2020).

[d] 10 m DEM (U.S. Geological Survey, 2020).

[e] Davis et al. (2015).

are predominantly underlain by sedimentary rocks, including sandstone and mudstone (California Department of Conservation and California Geological Survey, 2001; Kilbourne & Mata-Sol, 1983). Stream reaches in the S. Cascades are generally underlain by rocks of volcanic origin, such as andesite and basalt (California Geological Survey, 2015). The geologies in the Klamath Mountains and Sierra Nevada are more complex, with many of the rocks in each region originating from the collision of island arcs with the North American plate, which caused metamorphism of the overlying sedimentary and intermediate volcanic rocks and plutonic intrusions (Irwin & Wooden, 1999; Rinehart, Ross, & Pakiser, 1964). As such, stream reaches in the Klamath Mountains are underlain primarily by argillite, greenschist, and diorite rock types, while sites in the Sierra Nevada are underlain primarily by argillite and peridotite (California Geological Survey, 2015).

The overall climate of the study area is Mediterranean with 30-year normal annual precipitation ranging from 1,256 to 1,650 mm and 30-year mean annual air temperature between 9.5 and 12.9°C (Table 1; PRISM Climate Group, 2004). However, there are climate variations across geomorphic provinces. In the N. Coast, the dominant source of precipitation is low-intensity rainfall, with about 90% of the annual rainfall occurring between October and April. In the S. Cascades, between 67 and 74% of annual precipitation falls as snow between November and April. Similarly, most precipitation falls as snow in the Klamath Mountains and Sierra Nevada. Annual snow water equivalent (SWE) is, on average, 676 mm in the S. Cascades (SNOTEL Station ID: SMS), 499–689 mm in the Klamath Mountains (SNOTEL Station IDs: 341, MB3 and SCT), and ~962 mm in the Sierra Nevada (SNOTEL Station IDs: RCW & GOL; Table 1; USDA Natural Resources Conservation Service, 2020). In terms of temperature, the N. Coast is generally the warmest due its low elevation and close proximity to the Pacific Ocean with a 30-year mean of 12.9°C. The S. Cascade and Klamath Mountains regions, which are the highest in elevation, had the lowest 30-year mean air temperature of 9.5–10.2°C. The Sierra-Nevada region is intermediate to the other regions with a mean air temperature of 11.8°C.

All of the investigated reaches were located in forested catchments, which were dominated by coastal redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) in the N. Coast, ponderosa pine (*Pinus ponderosa*) and Douglas-fir in the S. Cascades and the Klamath, and by Douglas-fir, ponderosa pine, incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), and Sugar pine (*Pinus lambertiana*) in the Sierra Nevada. None of the watersheds included in our survey were recently burned or harvested and there was no evidence for water abstraction or diversion. The mean tree age across our study sites varied between 87 and 129 years (Davis et al., 2015, Table 1).

2.2 | Field data collection

We conducted field surveys in 101 headwater stream reaches between June and September 2018. We only selected Class II streams based on the California Forest Practices Rules (CAL FIRE, 2017), which are non-fish bearing tributaries of larger, fish bearing streams (Class I). Additionally, most of the selected streams drained a minimum of 40.5 ha in the Coast Forest District or 60.7 ha in the Northern and Southern Forest Districts, or had an average bankfull width greater than 1.5 m. In our site selection, we also avoided roads and road crossings to mitigate any potential confounding effect. To achieve this, we had to move the lowest downstream cross-section upstream ~0.03–1.8 km from the confluence for 45 streams. There were no road adjacency issues for any of the other streams. Pictures of representative sites are included in Figure S1.

Annual precipitation during the year of our study was 26–38% lower than normal in the Klamath and N. Coast regions (Table 1). Comparatively, annual precipitation in the S. Cascades and Sierra Nevada regions was within 6% of normal during our sampling campaign (PRISM Climate Group, 2004; Thornton et al., 2018). In 2018, mean air temperature was 0.01–1.1°C warmer compared to the long-term normal across the four regions (Table 1).

The length of each stream reach (>60 m) in our study was at least 20-times longer than its bankfull width. All reaches were located upstream from their confluence with a larger downstream receiving watercourse. Along each stream reach we measured bankfull dimensions at >10 cross-sections, which were evenly spaced along the reach length. At each cross-section, we quantified bankfull width by extending a topographic tape across the stream after visually identifying bankfull stage using typical indicators (e.g., break in slope, vegetation presence/absence, soil transitions, point bars or bank undercuts, stains on boulders/bedrock; Dunne & Leopold, 1978). We quantified bankfull depth at the centre of each section with a wading rod. At each cross-section, we also noted the presence or absence of water in the channel. We also quantified the grain size distribution (GSD) of the channel surface at a cross-section per site with a 100-pebble count (Wolman, 1954), which was then summarized in fractional sizes corresponding to the 16th (D_{16}), 50th (D_{50}), and 84th (D_{84}) percentiles. Finally, we georeferenced the location of each stream reach with a GPS unit (Garmin GPSMAP 64st, accuracy 3.65 m).

2.3 | Data analysis

2.3.1 | Flow permanence and network connectivity classification

Spatial differences in flow permanence and network connectivity were quantified based on field observations of the presence or absence of water. Specifically, we classified a stream as 'perennial' if we observed the presence of water in every cross-section throughout the entire reach length (Figure 2a). Alternatively, we classified a stream as 'non-perennial' if we did not observe flowing water in at least one cross-section (≥1 dry section; Figure 2a). The flow permanence classification provided information about water availability within the entire reach.

However, it did not distinguish streams that contributed surface water to downstream, fish-bearing tributaries. To classify the potential for a stream to influence downstream watercourses by draining to the larger watercourse during the summer low flow period, we considered a second classification to define network connectivity. Sites were classified as 'connected' if we observed surface streamflow in the cross-section that was in the furthest downstream location (Figure 2b). Conversely, we classified streams as 'disconnected' if we did not observe streamflow at the cross-section that was furthest downstream (Figure 2b).

2.3.2 | Flow permanence and network connectivity relationships with channel geometry and grain size

We investigated whether there were discernible relationships between either flow permanence or network connectivity and both channel geometry (i.e., bankfull width, bankfull depth) and surface GSD. We also quantified relationships between drainage area and both bankfull width and bankfull depth for perennial/non-perennial and connected/disconnected streams in each of the four geomorphic provinces. Given that the channel geometry and GSD variables were non-normally distributed ($p \leq .07$), we used non-parametric tests, including the Kruskal–Wallis test (Kruskal & Wallis, 1952) and Conover–Iman test (Conover & Iman, 1979) with Bonferroni corrections to avoid Type I error (Bonferroni, 1936).

2.3.3 | Controlling factors of flow permanence and network connectivity

To investigate controlling factors of flow permanence and network connectivity, we used random forest classification models (Breiman, 2001). Predictor variables in our models included six geomorphic characteristics of streams, which were measured in the field (i.e., channel size and GSD) and 11 geospatial features, which represented factors that potentially influenced the presence or absence of water in headwater streams (Table 2; Jaeger et al., 2019).

Prior to the analysis, we summarized the grain size data with a gradation coefficient, which expressed the spread of the distribution from percentiles and reflected the uniformity of the channel bed material (Bunte & Abt, 2001a, 2001b; Julien, 2010; Yang, 1996). Additionally, we computed the winter (sum of precipitation in November–February) and spring (sum of precipitation between March–May) precipitation inputs from the 2018 water year monthly precipitation to account for the effect of seasonal precipitation inputs on the presence/absence of water in the stream channels.

Random forests are decision tree models that facilitate classification of a response variable based on the interaction of independent variables (Breiman, Friedman, Stone, & Olshen, 1984; Strobl, Boulesteix, Kneib, Augustin, & Zeileis, 2008). Specifically, random forest classification models construct an ensemble of individual decision trees based on a dataset, where each tree makes a single class prediction. The predicted class with the most votes (i.e., most popular prediction) becomes the model prediction. Since random forest models combine the predictions from a large number of individual decision trees together, variance is reduced and model accuracy improved (Breiman, 2001). The decision trees in the model are grown based on a randomly selected subset of the data, called

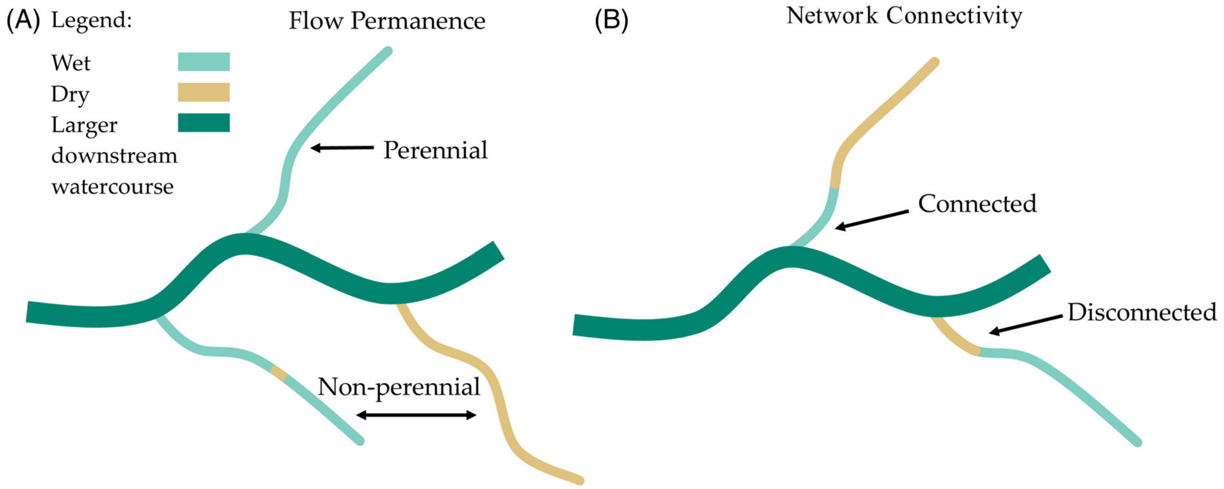

FIGURE 2 Conceptual diagram of (a) flow permanence classifications based on the presence (perennial) or absence (non-perennial) of surface flow at each cross-section throughout the entirety of the stream reach and (b) network connectivity classifications based on the presence (connected) or absence (disconnected) of surface flow within the furthest downstream cross-section of a reach, which drained into a larger downstream watercourse

TABLE 2 Variables included as predictors in the random forest models

	Variable name	Description	Units	Resolution	Reference/source
Field variables	Bankfull width	Channel dimensions at bankfull stage	m	0.01 m	—
	Bankfull depth		m	0.01 m	—
	Grain size distribution (GSD; D_{16}, D_{50}, D_{84})	16th, 50th, and 84th percentiles of the GSD	m	—	—
	gradation coefficient	Spread of the GSD from percentiles	mm	—	Bunte & Abt (2001a, 2001b)
Geospatial variables	Channel slope	Mean channel slope	m/m	10 m	Benda et al. (2007)
	Catchment slope	Mean catchment slope	m/m	10 m	Archuleta et al. (2017)
	Drainage area	To the downstream end of the reach	km^2	10 m	
	Elevation	Mean catchment elevation	m	10 m	
	Aspect	Mean catchment azimuth	°	10 m	
	Topographic wetness index	Mean for the catchment	—	10 m	(Beven & Kirkby, 1979)
	Precipitation	30-yr normal[a]	mm	800 m	PRISM Climate Group (2004)
		Monthly 2018[a] water year		1,000 m	Thornton et al. (2018)
	Temperature	30-year normal	°C	800 m	PRISM Climate Group (2004)
		Monthly 2018 water year		1,000 m	Thornton et al. (2018)

[a] We summarized precipitation inputs as relative winter (November–January) and relative spring (March–May) from the normal and 2018 monthly water year precipitation.

'bootstrapped' or training data. Model predictions are then tested against the data excluded from the bootstrapped data, called 'out-of-bag' (OOB) or test data. Since the out-of-bag data is not used to train the model and is composed of a random subset of the original dataset, it can be used to provide an unbiased assessment of the model performance. We used two random forest classifications to predict whether a given reach was perennial and whether a given reach was connected. In addition, we ran eight additional models to predict flow permanence and network connectivity within each of the four study regions.

Random forest models also provide a metric of importance for each variable by estimating the mean decrease in standardized OOB accuracy, which was calculated as the percent decrease of default classification error related to the inclusion of a given variable (Liaw & Wiener, 2002). We further interpreted each model using partial dependence plots that show the marginal effect of each independent variable in the variance of the response variable (i.e., whether a given reach was perennial or connected) while holding all other variables constant at their mean value (Friedman & Meulman, 2003). Partial dependence plots can be informative tools used to interpret random forest models as they describe the type of relationship (i.e., linear, monotonous, or more complex) between a given independent variable and the response variable class.

We set the number of decision trees for the models to build to 1,500. The number of randomly selected variables used to make each decision was set to five. Due to an imbalance in the number of perennial sites to non-perennial sites and connected to disconnected sites, we set the minimum sample size for each tree to represent the minimum number of a given class. All models were constructed in R (R Core Team, 2020) using the 'randomForest' package (Liaw & Wiener, 2002).

3 | RESULTS

3.1 | Flow permanence and connectivity classification

In summer 2018, our field surveys across four geomorphic provinces in Northern California indicated more non-perennial streams (at least one dry cross-section) than perennial streams (continuous stream flow across all cross-sections) in the S. Cascades, N. Coast, and Sierra Nevada regions. Specifically, in the S. Cascades 69% (18 of 26) of the streams were non-perennial with 54% (14 of 26) of streams being completely dry along all cross-sections (Figure 3). Similarly, in the N. Coast 68% (17 of 25) of the streams were non-perennial while in the Sierra Nevada 60% (15 of 25) of the streams were non-perennial. In contrast to the S. Cascades, in the N. Coast only one non-perennial stream was completely dry while in the Sierra Nevada only seven of the non-perennial streams were completely dry (Figure 3). The Klamath Mountains had the most perennial streams – only 32% (8 of 25) of the streams were non-perennial and only two were dry along all cross-sections (Figure 3).

Our field surveys also identified stream network connectivity based on the presence of surface water in the most downstream cross-section we surveyed. Streams in the Klamath Mountains were the most connected (21 of 25; 84%) followed by streams in the N. Coast (20 of 25; 80%; Figure 4). In contrast, less than half of the streams in both the Sierra Nevada (12 out of 25; 48%) and S. Cascades (12 of 26; 46%) were connected and drained to a larger downstream reach (Figure 4).

Overall, 62% (693 of 1,121) of all the surveyed cross-sections across the study area contained surface water (Figure 3). Streams in the Klamath Mountains supported the largest proportion of wet cross-sections (216 of 264; 82%). In comparison, we found surface water in 74% (204 of 275) of the cross-sections in the N. Coast and in 60% (163 of 271) of the cross-sections in the Sierra Nevada region. In contrast, we found surface water in only 35% (110 of 311) of the cross-sections in the S. Cascades region.

3.2 | Channel geometry across regions and stream classifications of flow permanence and network connectivity

Median channel dimensions varied across the four regions. The median bankfull widths were widest in the S. Cascades (3.05 m) followed by Sierra Nevada (2.48 m), Klamath (1.73 m), and the N. Coast (1.49 m). Similarly, the bankfull depths were deepest in the S. Cascades (0.59 m) followed by Sierra Nevada (0.49 m), Klamath (0.35 m), and the N. Coast (0.35 m). Statistically, there was strong evidence (χ^2 = 41.4–50.8, $p < .01$) that the stream channels in both the S. Cascades and Sierra Nevada were wider and deeper than the stream channels in the Klamath Mountains and N. Coast regions (Table S1). Comparatively, the stream channels in the S. Cascades and Sierra Nevada had similar bankfull widths (p = .39, Table S1) and depths (p = 1.0 Table S1). Likewise, the stream channels in the Klamath Mountains and the N. Coast had similar bankfull widths (p = 1.0, Table S1) and depths (p = 1.0, Table S1).

We also compared the stream channel dimensions between perennial versus non-perennial and connected versus disconnected streams. Interestingly, across all four regions the perennial reaches were ~17% narrower (χ^2 = 3.6, p = .058) and ~19% shallower (χ^2 = 7.0, p = .008) than non-perennial streams (Table 3 and Table S2). However, within each region there was no evidence for differences in the bankfull widths or depths between perennial and non-perennial reaches (Table S3). Similarly, across all four regions, the connected stream reaches were ~38% narrower (χ^2 = 10.8, p = .001) and ~26% shallower (χ^2 = 13.6, p = .0002) than disconnected stream reaches (Table S2). Again, within each of the individual regions there was no evidence for differences in bankfull depths or widths between the connected and disconnected streams (Table S3).

We also analysed the regression relationships between drainage area and channel dimensions (bankfull width and bankfull depth) for the perennial versus non-perennial and connected versus disconnected streams. Across all four regions, there was moderate to strong evidence for a direct relationship between drainage area and channel width for both the perennial (r^2 = .30, $p < .0001$) and non-perennial (r^2 = .07, p = .038) streams (Figure 5a). Interestingly, non-perennial streams tended to have slightly wider stream channels for a given drainage area relative to the perennial streams. However, statistically there was no evidence that the relationships were different between the perennial and non-perennial streams (p = .42). Similarly, in perennial streams the channel depth tended to increase with drainage area (r^2 = .22, p = .0013), while in non-perennial streams there was no evidence for a relationship between channel depth and drainage area (Figure 5b). Across all hydrologically connected streams in the four regions we also observed increasing stream channel widths (r^2 = .25, $p < .0001$; Figure 5c) and depths (r^2 = .16, p = .0011; Figure 5d) with increasing drainage area. Alternatively, across all disconnected streams there was no evidence for a relationship between drainage area and stream channel widths or depths.

Within the individual regions we observed relationships between drainage area and bankfull width or bankfull depth in the perennial streams in the Klamath and Sierra Nevada regions. Specifically, in

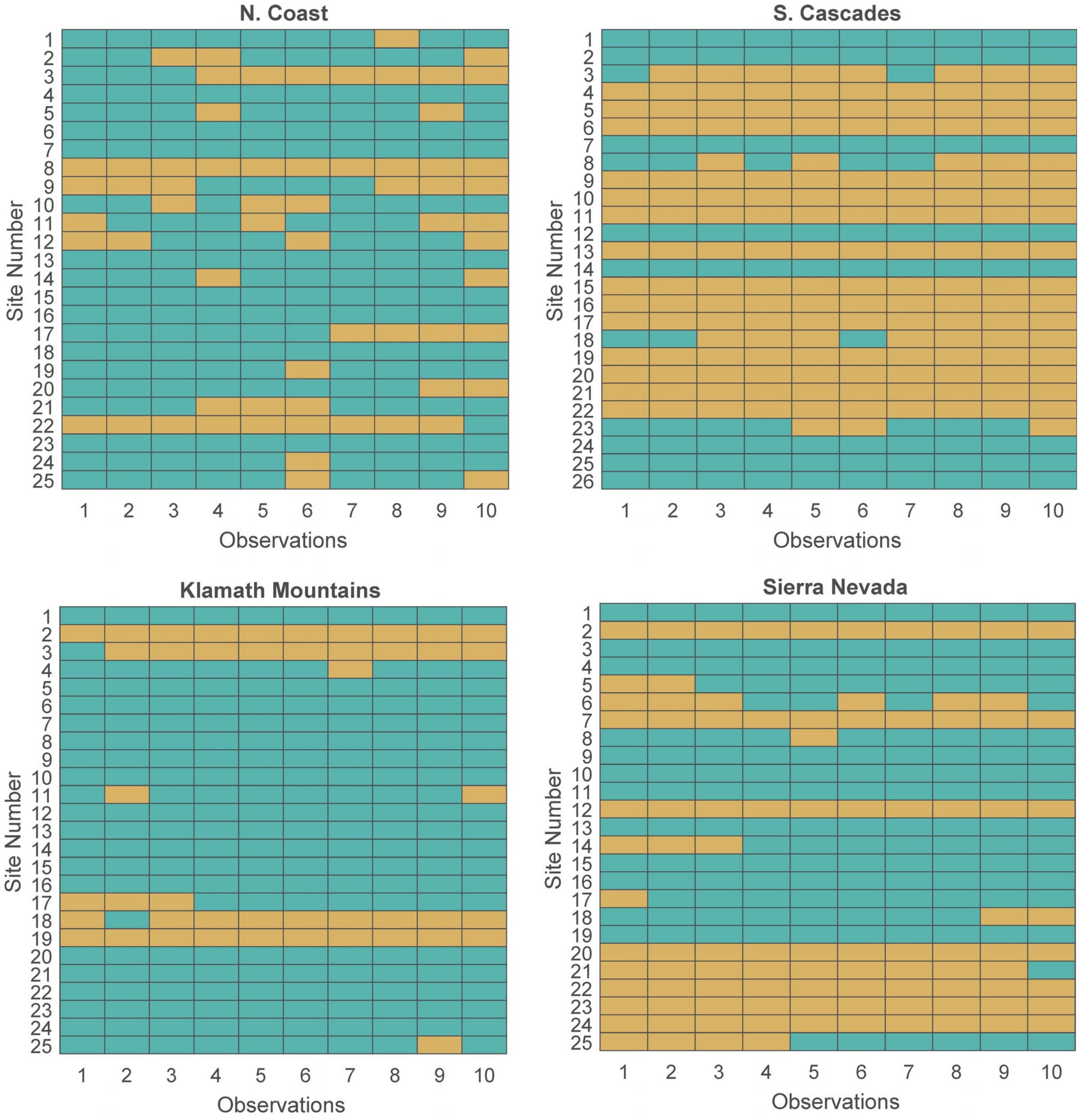

FIGURE 3 Heat maps illustrating spatial variability in flow permanence and network connectivity across four geomorphic provinces. The *x*-axis refers to the first 10 cross-sectional observations along a reach and the *y*-axis refers to each individual stream reach per geomorphic province. Each rectangle (i.e., cross-section) is coloured according to either the presence (teal) or absence (sand) of water during the time of observation. Within each geomorphic province, the reaches are presented in the chronological order in which they were surveyed

perennial streams of the Klamath Mountains region, there were positive relationships between drainage area and both bankfull width (r^2 = .52, p = .001) and bankfull depth (r^2 = .34, p = .013). In perennial streams in the Sierra Nevada region there were also positive relationships between drainage area and both bankfull width (r^2 = .61, p = .008) and bankfull depth (r^2 = .59, p = .009; Figure S1). In contrast, there was no evidence for relationships between drainage area and either bankfull width or bankfull depth in the perennial streams of the S. Cascades or N. Coast regions nor in the non-perennial streams within each of the four regions (r^2 = .01–.13, p = .38–.78; Figure S1).

Similarly, we only observed relationships between drainage area and bankfull width or bankfull depth in the hydrologically connected streams in the Klamath and Sierra Nevada regions. Specifically, in connected streams of the Klamath Mountains region, there were positive relationships between drainage area and both bankfull width (r^2 = .28, p = .013) and bankfull depth (r^2 = .49, p < .0001). In connected

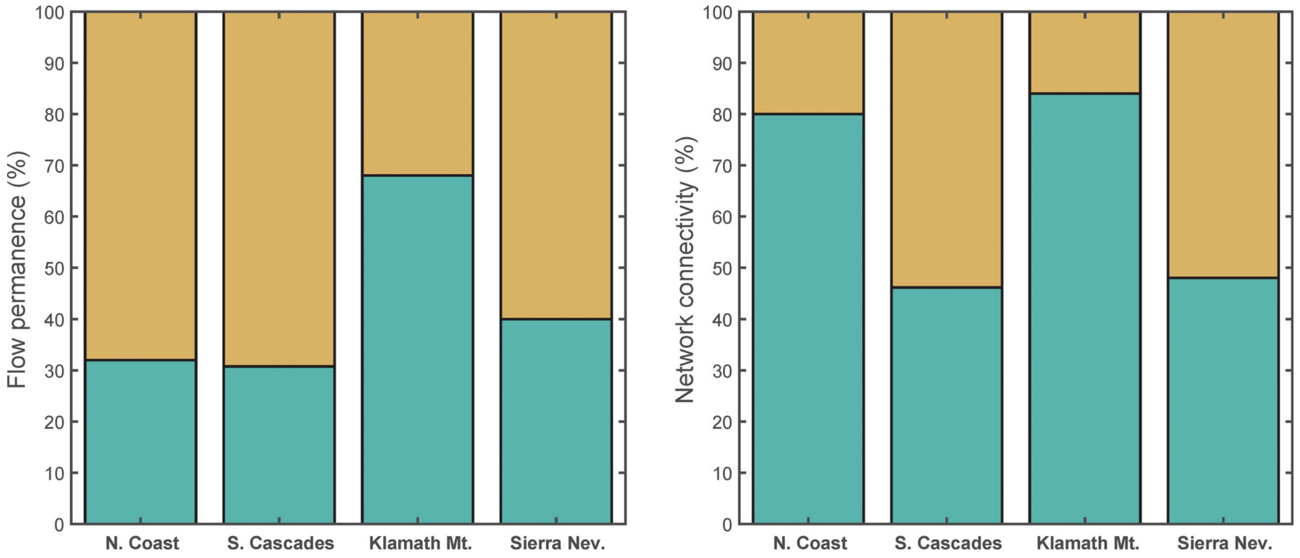

FIGURE 4 Percentage of sites per classification and geomorphic province. The lower (teal) shading represents the connected or perennial sites, while the upper (sand) shading represents disconnected or non-perennial sites

TABLE 3 Summary of median channel dimensions and grain size across geomorphic provinces and flow permanence and flow connectivity classifications

		Channel size (m)		Grain size (mm)				
Region	Classification	Width	Depth	D_{16}	D_{50}	D_{84}	DA (km^2)	No.
N. Coast	Perennial	1.50	0.35	5	11	24	0.53	8
	Non-perennial	1.49	0.35	7	13	22	0.33	17
	Connected	1.58	0.35	6	12	24	0.40	20
	Disconnected	1.46	0.37	6	10	22	0.24	5
S. Cascades	Perennial	3.05	0.53	15	32	67	0.88	8
	Non-perennial	3.04	0.59	31	61	121	0.55	18
	Connected	3.05	0.57	16	33	68	0.64	12
	Disconnected	3.04	0.59	32	65	121	0.54	14
Klamath Mtns.	Perennial	1.73	0.34	13	27	51	0.63	17
	Non-perennial	1.77	0.38	16	26	46	0.58	8
	Connected	1.73	0.35	13	26	54	0.63	21
	Disconnected	1.86	0.37	17	25	39	0.41	4
Sierra Nevada	Perennial	1.89	0.42	12	25	49	0.51	10
	Non-perennial	2.66	0.55	23	38	72	0.43	15
	Connected	1.89	0.46	12	26	52	0.44	12
	Disconnected	2.81	0.55	24	39	84	0.43	13
All regions	Perennial	2.00	0.39	13	26	50	0.63	43
	Non-perennial	2.33	0.47	17	30	56	0.43	58
	Connected	1.94	0.39	12	24	45	0.57	65
	Disconnected	2.67	0.49	24	40	75	0.38	36

streams in the Sierra Nevada region there were also positive relationships between drainage area and both bankfull width (r^2 = .49, p = .011) and bankfull depth (r^2 = .47, p = .014; Figure S2). In contrast, there was no evidence for relationships between drainage area and either bankfull width or bankfull depth in the connected streams of the S. Cascades or N. Coast regions nor in the disconnected streams within each of the four regions (r^2 = .02–.14, p = .10–.58; Figure S2).

3.3 | Channel grain size variability across regions and flow permanence and network connectivity classifications

Regional comparisons of stream channel GSDs for all size fractions (D_{16}, D_{50}, and D_{84}) were generally ranked as: S. Cascades > Sierra Nevada > Klamath Mountains > N. Coast (Table 3). For example, the

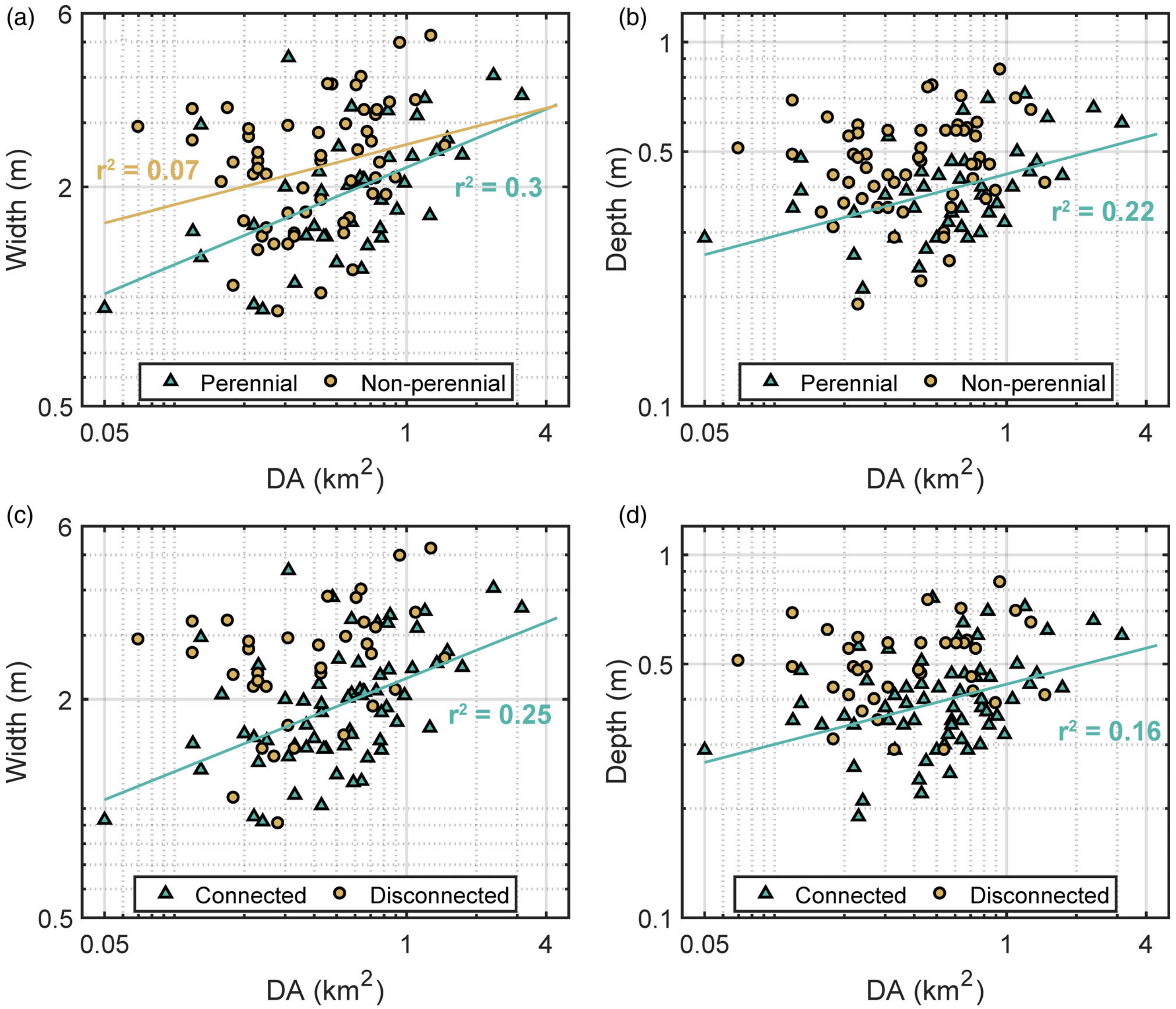

FIGURE 5 Channel geometry relations for perennial and non-perennial sites (a, b) and connected and disconnected sites (c, d) across the study area. Panels a and c show the relationship between drainage area and bankfull width and panels b and d show the relationship between drainage area and bankfull depth. A trend line is provided if there was statistical evidence (p < .05) for a relationship between the plotted variables

median grain size (D_{50}) was 52 mm in the S. Cascades, 32 mm in the Sierra Nevada, 26 mm in the Klamath Mountains, and 11 mm in the N. Coast (Table 3). Statistically, there was strong evidence that the grain size was finer in all size fractions in the N. Coast compared to the other three regions (χ^2 = 45.5–53.7, p = <.001–.015, Table S1). There was also all strong evidence that the channel sediment particles were coarser in the S. Cascade stream reaches compared to both the Klamath Mountains (p = .0011–.0045) and N. Coast regions (p < .001; Table S1). Alternatively, there was no evidence for differences in the GSDs (D_{16}, D_{50}, or D_{84}) in the Sierra Nevada compared to either the Klamath Mountains (p = .50–.91) or the S. Cascade regions (p = .13–.36; Table S1).

In comparisons between streams grouped by stream permanence classification, perennial streams had 11–26% finer GSDs than non-perennial streams (Table 3). Statistically, there was strong evidence (p = .01) the perennial reaches had a finer D_{16} than non-perennial reaches (Table S2). However, there was only suggestive evidence the D_{50} (p = .06) and D_{84} (p = .16) size fractions were finer in the perennial streams compared to the non-perennial reaches across the four regions (Table S2). Within individual regions, there was strong evidence that channel grain size in all size fractions (D_{16}, D_{50} or D_{84}) was finer in perennial stream reaches compared to non-perennial reaches in both the S. Cascade (p = .019–.043) and Sierra Nevada (p = .020–.041) regions (Figure 6, Table S3). However, there was no evidence for differences in the GSDs between perennial and non-perennial stream reaches in either the N. Coast or Klamath Mountain regions (Figure 6, Table S3).

In comparisons between streams grouped by network connectivity, connected stream reaches had 20–50% finer GSDs than disconnected stream reaches (Table 3). Statistically, there was strong

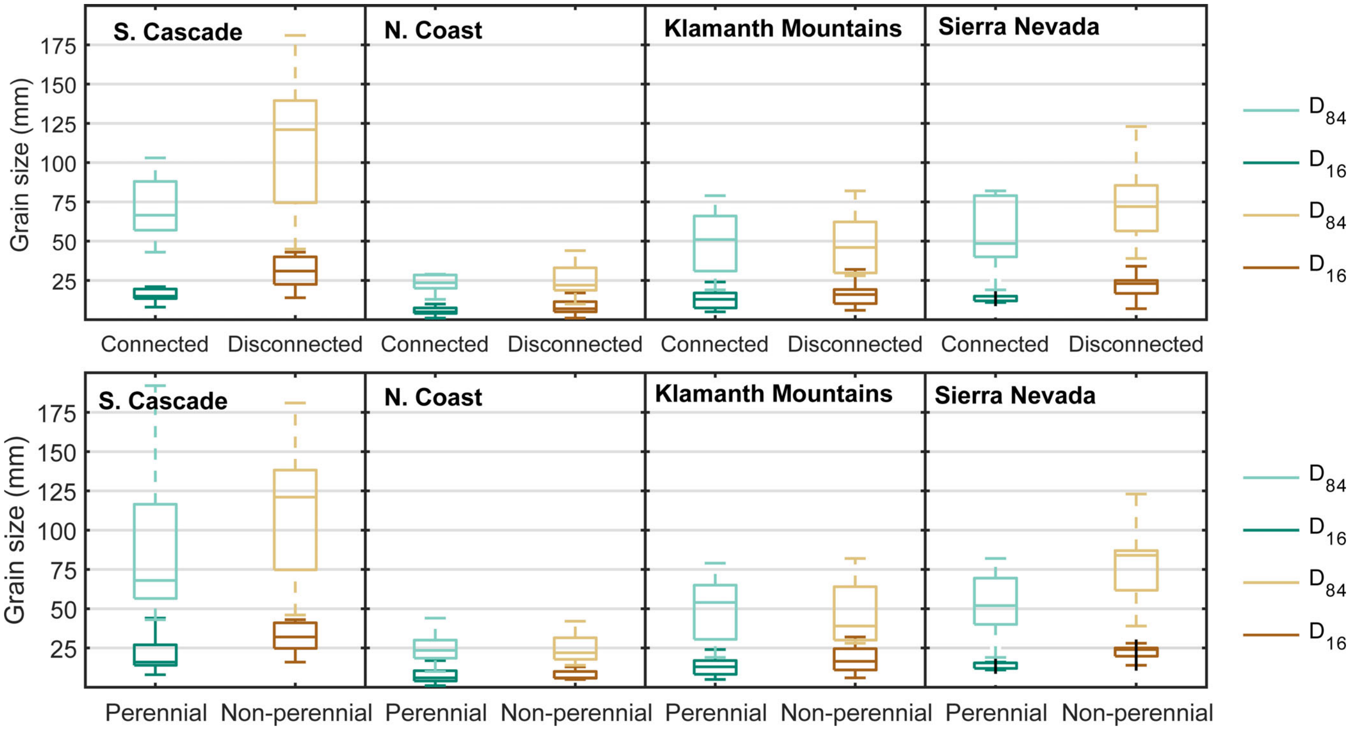

FIGURE 6 Distribution of grain sizes (D_{16} and D_{84}) across connected and disconnected sites and perennial and non-perennial sites in each geomorphic province. The top and bottom of each box are the 25th and 75th percentiles of the distribution and the middle line inside the box is the median value. Lines extending out of the box correspond to the maximum and minimum values

evidence ($p < .001$) the connected reaches had finer grain size in all size fractions (D_{16}, D_{50}, and D_{84}) compared to the disconnected streams across all four regions (Table S2). Within the individual regions, there was strong evidence that channel grain size in all size fractions (D_{16}, D_{50}, or D_{84}) was finer in connected stream reaches compared to disconnected reaches in the Sierra Nevada ($p = .009$–$.015$; Figure 6, Table S3). In the S. Cascades, there was only evidence that the connected streams had finer D_{16} ($p = .025$) and D_{50} ($p = .019$) compared to disconnected streams (Figure 6, Table S3). However, there was no evidence for differences in grain size fractions between connected and disconnected stream reaches in either the N. Coast or Klamath Mountain regions (Figure 6, Table S3).

3.4 | Factors influencing flow permanence and network connectivity

To determine the relative importance of potential controlling factors of flow permanence and network connectivity we developed two random forest models. Input variables to our supervised machine learning models, included: (a) field-based variables of channel form and stream bed sediment size, (b) geospatial variables related to catchment physiography and hydrology, and (c) climatic variables (Table 2, Figure S4). The best random forest model for classifying perennial and non-perennial streams had an overall accuracy of 73.2%. Comparatively, the best random forest model at classifying connected and disconnected streams had an overall accuracy of 76.3%.

In our model to assess the controlling factors of flow permanence, the four most important predictor variables were D_{16}, winter 2018 precipitation, drainage area, and D_{84} with a total mean decrease in standardized OOB accuracy of 40.2% if all four of these variables were removed from the model (Figure 7). The omission of D_{16} alone from the model would result in a 12% mean decrease in standardized OOB accuracy. Removing the second-forth most important variables would result in 8.4–10.8% decreases in the standardized OOB. There were five other variables that would have produced at least a 5% decrease in the standardized OOB accuracy if removed from the flow permanence model, including channel gradient (7.5%), mean elevation (5.9%), sediment gradation coefficient (5.9%), bankfull depth (5.7%), and mean air temperature (5.1%). Eight of our variables were generally poor predictors of flow permanence in our model – removal of any of the remaining variables from the model would have resulted in more modest decreases of overall OOB accuracy between 1.5 and 4.6% (Figure 7).

In our model to assess the controlling factors of network connectivity, the four most important predictor variables were winter 2018 precipitation, D_{16}, spring 2018 precipitation, and bankfull depth (Figure 7). The removal of these four variables from the model would have resulted in a total mean decrease in standardized OOB accuracy of 57% (Figure 7). In particular, removal of either winter 2018 precipitation or D_{16} would have resulted in a decrease in standardized OOB accuracy of >17.8%. The removal of the third and fourth most important variables would result in 9–11% decreases in the standardized OOB. There were six variables that would have produced at least a

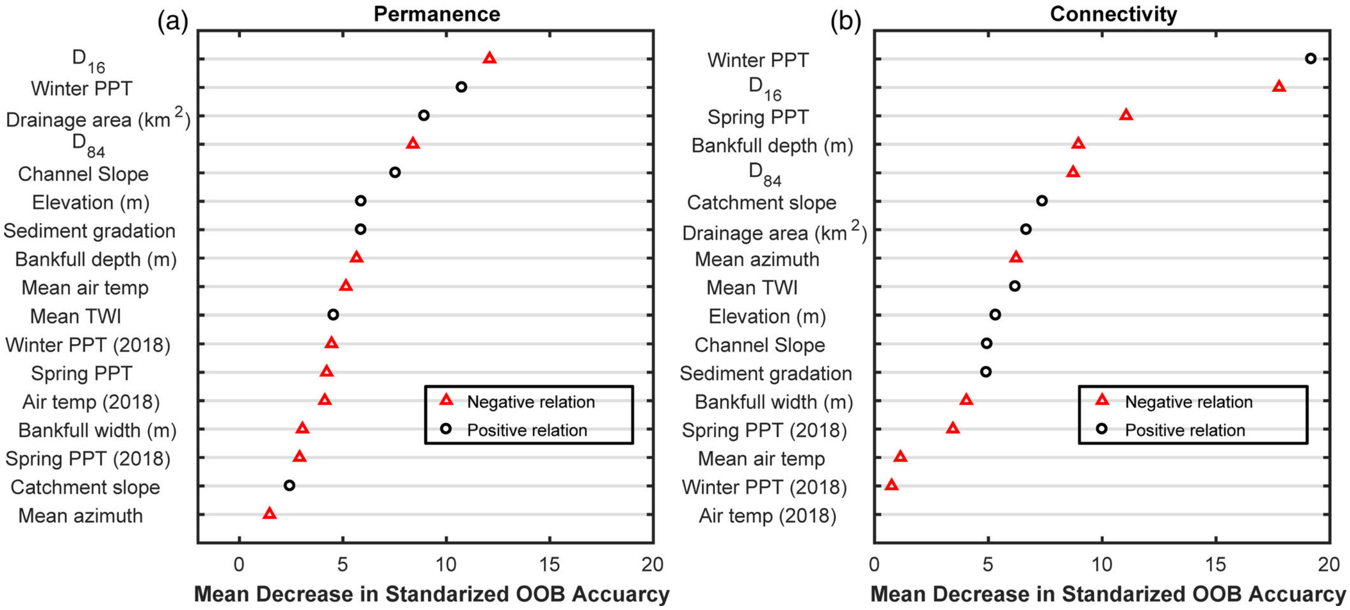

FIGURE 7 Variable importance plots of modelled covariates as a function of standardized mean decrease in out-of-bag (OOB) accuracy for (a) flow permanence and (b) network connectivity. Markers indicate if the relationship between a covariate and the likelihood of a site being perennial or connected was positive or negative as inferred from partial dependence plots

5% (5.3–8.7%) decrease in the standardized OOB accuracy if removed, including D_{84}, catchment slope, drainage area, azimuth, topographic wetness index, and elevation. The removal of any of the remaining seven variables from the model would have resulted in smaller decreases (0.75 and 4.9%) in OOB accuracy (Figure 7).

While the relative importance of the 17 independent variables considered in the models to predict flow permanence and network connectivity was slightly different between the two models, the partial dependency plots indicated the same directionality in the relationships between the covariates and the likelihood of streams being perennial or connected. The analysis of partial dependency plots indicated that the likelihood of a stream being classified as perennial or connected was positively related to winter precipitation, drainage area, channel slope, elevation, sediment gradation, topographic wetness index, and catchment slope (Figure 7). In contrast, the likelihood of classifying a stream as perennial or connected was negatively correlated with grain size (D_{16}, D_{84}), channel dimensions (bankfull depth and width), mean air temperature, winter and spring precipitation, and azimuth (Figure 7).

The regional models indicated that no single variable was the most relevant across all regions at predicting flow permanence (Figure S5). Field derived variables were, on average, more important than geospatial variables at predicting flow permanence. For example, channel grain size (D_{84}) was consistently the fourth to sixth most important variable across all regions, sediment gradation was the first to third most important variable in two of the regions, and channel dimensions ranked approximately seventh across all regions. Among the geospatial variables, catchment slope was an important flow permanence predictor across all regions, ranking between second to seventh. The importance of the climate related variables varied widely with ranks between first and 1seventh (Figure S5).

Similarly, the regional models also indicated that no single variable was the most relevant across all regions at predicting network connectivity (Figure S6). Within the regional models the mean rank of the field derived variables (9.3) was similar to the mean rank of the geospatial variables (8.9). Channel dimensions ranked, on average, approximately seventh at predicting network connectivity across all regions. The rank of the channel grain size variables (D_{16} and D_{84}) varied widely, between 3rd and 17th. Among the geospatial variables, elevation was ranked third to fourth in the N. Cascade and Cascade regions and 15th to 17th in the Klamath and Sierra. In the Sierras Nevada region, channel and catchment slopes were the most important variables, ranking first and second. Mean air temperature was also ranked highly at predicting networking connectivity, ranging from first to fifth, across all regions (Figure S6).

4 | DISCUSSION

4.1 | Factors influencing flow permanence and network connectivity

In our analysis of >1,000 cross-sections from 101 streams in Northern California, we found that streamflow permanence and network connectivity were strongly driven by regional climate. While this was not surprising, it was interesting that the dominant climatic variable in our analysis was the proportion of annual precipitation that fell during winter (Figure 7). For example, in our study the Klamath and Sierra Nevada regions had the greatest number of perennial streams. While rain is generally the dominant source of precipitation across all our study regions, the fraction of precipitation as snow is generally greater in the Klamath and Sierra Nevada relative to the other two study regions (Lane, Dahlke, Pasternack, & Sandoval-Solis, 2017; Zheng, Wang, Zhou, Sun, & Li, 2018).

Precipitation has previously been described as a major control of surface water (Buttle et al., 2012; Costigan et al., 2016; Levick et al., 2008). In a study by Li, Wrzesien, Durand, Adam, and Lettenmaier (2017), they illustrated that the majority of total runoff in the Western US was derived from snowmelt, even in sub-regions where snowfall represented a smaller fraction of the total annual precipitation. Indeed, precipitation has been noted as a key driver of flow permanence across other regions, including headwater streams in the Pacific Northwest (Jaeger et al., 2019), Kentucky, Ohio, and Indiana (Fritz et al., 2008), Spain (González-Ferreras & Barquín, 2017), and tropical systems in Panama (Zimmermann, Zimmermann, Turner, Francke, & Elsenbeer, 2014). Interestingly, Hunter, Quinn, and Hayes (2005) found that the occurrence of summer streamflow in small, headwater catchments in southwest Washington was determined by spring precipitation, rather than winter precipitation. However, we posit that temporally concentrated precipitation during winter, accumulation and persistence of a snowpack, and the timing of snowmelt was a likely determinant of the proportion of annual precipitation that recharged catchment storage in our study streams, influencing the longer-term presence or absence of streamflow (Barnhart et al., 2016; Sando & Blasch, 2015; Webb, Wigmore, Jennings, Fend, & Molotch, 2020; Zheng et al., 2018). This is supported by our additional observations that the long-term normal winter precipitation was a stronger predictor of streamflow permanence than the precipitation falling during the year of our study and highlights the importance of antecedent conditions and groundwater recharge/storage (Doering, Uehlinger, Rotach, Schlaepfer, & Tockner, 2007; Konrad, 2006). In our sites, the importance of winter precipitation is most likely due to the accumulation and persistence of a snowpack, which can provide an important source of water to headwater streams during the summer low flow period. Indeed, Sando and Blasch (2015) also found snowpack persistence to be critical for flow permanence in the Rocky Mountains. Interestingly, they also noted the importance of knowing where snowpack is a dominant driver of streamflow permanence to facilitate future forest management efforts given climate projections for the western US (Mote, Li, Lettenmaier, Xiao, & Engel, 2018; Sando & Blasch, 2015).

We also speculate that some of the variability in flow permanence and network connectivity across our study region was driven by differences in subsurface geology. For example, we observed the most wet cross-sections and greatest connectivity in the Klamath and N. Coast regions, which are dominated by sedimentary and metasedimentary geology, which support relatively high groundwater storage (Keppeler & Cafferata, 1991). Alternatively, the sites we visited in the S. Cascades were underlain by fractured-rock aquifers of volcanic origin (e.g., basalt and andesite) and the sites we visited in the Sierra Nevada region were primarily underlain by sedimentary (argillite) and igneous rocks (peridotite), which have comparatively small storage (Ferriz, 2001; Lane et al., 2017). Even in locations in the Cascades region where groundwater recharge is substantial, the landscape is generally highly dissected, producing many large springs, which can contribute to discontinuous channelized streamflow (Manga & Kirchner, 2004). Previous efforts to map active channel length along headwater stream networks have illustrated that the presence of groundwater seeps can create substantial heterogeneity in both subsurface processes and surface flow (Asano, Uchida, & Ohte, 2002; Binley et al., 2013; Payn, Gooseff, McGlynn, Bencala, & Wondzell, 2012; Whiting & Godsey, 2016). Similarly, Godsey and Kirchner (2014) observed substantial contraction and disconnection of three headwater streams in the Sierra Nevada Mountains during the summer low flow period. Thus, given the regional characteristics of the Sierra Nevada, the high stream discontinuity was not unexpected. Similarly, given the subsurface geology and prevalence of groundwater seeps in the S. Cascades, it was not surprising that we observed the fewest perennial streams, connected streams, and wet cross-sections in that region, despite a similar precipitation regime as the Klamath and Sierra Nevada regions.

Comparatively, in the N. Coast region the critical zone is often deep and composed of friable argillite and sandstone, which has high water storage capacity (Hahm et al., 2019). However, soil pipes and pipeflow are known to play a critical role for runoff generation in this region (Keppeler & Brown, 1998). Soil pipes and associated macropores generally deliver water rapidly to streams and cease to flow in the dry summer period because they have little potential for long-term water storage (Beven & Germann, 2013; Hunter et al., 2005). Additionally, high erodibility of the geology in the Coast region is conducive to many prominent knickpoints in the stream channels, which contribute to high infiltration into thick gravel deposits in the channel bed leading to high discontinuity in channelized flow in the region (Lovill, Hahm, & Dietrich, 2018). Indeed, streams in the N. Coast region were the most intermittent, with only 30% of streams observed as perennial.

As expected, we also found a positive relationship between both streamflow permanence and network connectivity and drainage area across all four study regions (Figure 7). This was consistent with previous studies in forested headwater streams in the United States (Fritz et al., 2008), as well as in large basins in France and in Spain (González-Ferreras & Barquín, 2017; Snelder et al., 2013) that found the presence of streamflow was related to the contributing area. Similarly, we found that channel depth was a moderately important predictor of flow permanence and connectivity (Figure 7). However, there were poor relationships between channel width and both streamflow permanence and network connectivity. Interestingly, previous research in 12 headwater catchments across four geomorphic provinces in the Appalachian Highlands of south-eastern USA, Jensen, McGuire, and Prince (2017) found an inverse relationship between bankfull width and the occurrence of channelized flow. Alternatively, they did not find strong evidence for a relationship between bankfull depth and the occurrence of streamflow (Jensen et al., 2017). The relatively poor relationship between channel dimensions and flow permanence or network connectivity in our study was likely due to stronger relationships between channel dimensions and flow magnitude during large flood events that exceed bankfull discharge (Montgomery & Buffington, 1997). Thus, it was not entirely surprising there was a poor relationship between channel dimensions and the presence or absence of water in the surveyed channels during the summer low flow period.

Across all four of our study sub-regions the relationships between channel size (channel width and channel depth) and drainage area were also weak (Figure 5). The weak channel geometry relationships in these headwater streams were not entirely surprising, considering the constraints that steep channel gradients and larger grain sizes can impose on the channel geometry of mountainous streams (Heede, 1972; Wohl, Kuzma, & Brown, 2004). Additionally, while strong relationship between drainage area and channel size have been observed in many rivers, these have generally been in higher order river systems (Ferguson, 1986; Gleason, 2015; Leopold & Maddock, 1953; Parker, Wilcock, Paola, Dietrich, & Pitlick, 2007). Despite relatively few studies in headwater streams, some have found agreement with the relationships between drainage area and channel size in small headwater catchments (Brummer & Montgomery, 2003; Vianello & D'Agostino, 2007). However, similar to our study, Montgomery and Gran (2001) also found weaker channel geometry relations for small (<0.1 km^2) mountain streams in Oregon relative to larger streams. Additional analysis of each of the stream classifications (e.g., perennial, non-perennial, connected, disconnected) independently indicated slightly stronger relationships between drainage area and channel size for perennial streams and connected streams than for non-perennial and disconnected streams. However, these channel relationships were still surprisingly weak. The weakness in the channel geometry relationships likely reflects the importance of local controls on channel form, such as slope, grain size, and large wood, which have all been shown to influence the local occurrence of surface flow (Grizzel & Wolff, 1998; Hunter et al., 2005; Wohl et al., 2004). Additionally, the weak relationship across the four regions could reflect a strong lithologic control over the channel characteristics (Parida, Tandon, & Singh, 2017).

Flow permanence and network connectivity was also strongly related to the particle size distribution of the stream channel sediment across the four sub-regions. In general, streams cross-sections that were characterized by finer sediment were more likely to be perennial or connected compared to reaches with coarser sediment. Interestingly, in the Klamath and N. Coast regions, which tended to have the most connected streams and wet cross-sections, there were no differences in any of the GSDs (D_{16}, D_{50}, D_{84}) between perennial and non-perennial streams or between connected and disconnected streams. Alternatively, in the Cascade and Sierra Nevada regions, which were more disconnected and had fewer wet cross-sections, all three sediment size fractions were different between our stream classifications. We posit that streambeds with coarser GSDs were more permeable with greater hydraulic conductivity, leading to increased subsurface flow, groundwater recharge, and overall shorter catchment residence times (Brummer & Montgomery, 2003; Packman & Salehin, 2003; Sawyer & Cardenas, 2009; Ward et al., 2013). This is consistent with the perceptual model of the dominant hydrologic processes driving river corridor flow in mountain streams (Ward, Schmadel, & Wondzell, 2018), as well as previous work describing the role of groundwater-surface water interactions, hyporheic exchange, subsurface flow mechanisms in influencing streamflow in headwater catchments (Bencala, Gooseff, & Kimball, 2011; Castro & Hornberger, 1991; Godsey & Kirchner, 2014). Observations of high thermal responsivity of streams with coarse-textured substrates and low thermal responsivity of streams with fine textured substrates (Janisch et al., 2012) also supports the importance of channel grain size for determining the proportion of channelized flow.

Our results also implied that catchment physiography may partially explain some of variability in flow permanence and network connectivity. In particular, channel slope was the fifth most important variable in the flow permanence model, while catchment slope was the sixth most important variable in the network connectivity model. Research in the Pacific Northwest region also illustrated that channel and catchment slope were moderately important predictor variables of streamflow permanence, with climatic factors exerting the dominant control (Jaeger et al., 2019). The increasing likelihood of streamflow in steeper catchments and channels is consistent with strong hillslope hydraulic gradients in headwater catchments, resulting in a higher water table near the channel (Sklash & Farvolden, 1979; Voltz et al., 2013). Indeed, previous research has suggested that the internal topographic arrangement of a catchment may be a dominant control on water transit time from hillslopes to streams (McGuire et al., 2005). In a study including mountain streams in California, Oregon, and Idaho, Prancevic and Kirchner (2019) also found that topography (i.e., slope, catchment curvature, contributing drainage area) was a dominant control over flow partitioning and the expansion or retraction of stream networks.

4.2 | Implications for future research

In our study, we illustrated the used of random forest models to facilitate interpretation of the processes that control flow permanence and downstream flow connectivity in small, forested headwater streams. Our application of random forest models was different from previous efforts that have used them in the context of flow permanence modelling and prediction over a wider range of catchment sizes in Spain (González-Ferreras & Barquín, 2017) and the Pacific Northwest, USA (Jaeger et al., 2019). However, we demonstrated that random forest models offer a flexible and robust alterative to investigate the controlling factors of flow permanence in small headwater streams. Indeed, the accuracy of our flow permanence model (73.2%) was greater than the accuracy of the National Hydrography Dataset (NHD) for which Fritz, Wenerick, and Kostich (2013) reported that the misclassification of headwater streamflow class can be as high as 50%. Thus, random forest models may offer a useful alternative to future investigations of flow permanence in mountainous headwater streams.

5 | CONCLUSIONS

We used field observations from 101 headwater streams across four geomorphic provinces in Northern California during the summer low flow period in 2018 to quantify flow permanence and network connectivity. Additionally, we investigated potential drivers of flow permanence and network connectivity across the four regions. We found strong differences in the occurrence of perennial and connected streams across the regions, which appeared to be related to differences in channel substrate grain size, winter precipitation, drainage area, and bankfull depth. Our study illustrated the complexity of the processes that drive surface flow during the summer low flow period and highlighted the uncertainty in projecting flow permanence in streams across diverse regions. Despite the logistical and monetary costs associated with this type of field research, we must continue to improve our understanding of the processes driving flow permanence across space and time. Such efforts are necessary to facilitate informed land and water management and policy in forested headwater streams.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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