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Never the same river twice: On the causes and consequences of stream drying across space and time

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Never the same river twice:
On the causes and consequences of stream drying across space and time

By

Hana Moidu

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:
Professor Theodore Grantham, Chair
Professor Stephanie Carlson
Professor Albert Ruhi

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Abstract

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Rivers act as dynamic forces that shape Earth's changing surface, and whose scars we can still see punctuating our landscapes. Characteristically everchanging, they have inspired many poets, thinkers, and wanderers with their mutable nature. The quote "no man steps in the same river twice, for it is not the same river and he is not the same man" – attributed to the Ancient Greek philosopher Heraclitus – is known to be true for anyone who has seen a river swell beyond its banks, only to watch it shrink back to a narrow passage. But what about the streams that dry? The temporary, the seasonal, the irregular, the ephemeral, the discontinuous? These waterways, termed in this dissertation as 'intermittent', periodically, and naturally, cease to flow. They are similarly unpredictable, where the patterns and extent of drying are highly variable, with some reaches going dry year after year, regardless of previous conditions, while others respond more proportionally to the amount of antecedent rainfall. While riverine theory and study has been traditionally based on perennial model systems, recognition of the importance of intermittent streams has grown in recent years. However, critical gaps remain around the causes and consequences of intermittent stream drying across space and time. These systems are especially sensitive to climate fluctuations, and there is considerable potential for such ecosystems, and the species and services they support, to shift in response to climate change. Yet, relatively little attention has been given to identifying and evaluating the factors that influence variability in intermittent stream drying. Without documenting how intermittent streams vary within and across years, an essential component of their character is lost. With increasing precipitation volatility and rising temperatures, there is an urgent need to characterize where and when intermittent streams will be buffered from, or vulnerable to, altered climate conditions. In this dissertation, I explore the causes and consequences of intermittent stream variability, with a focus on the interannual variation in the hydrological and ecological patterns within these systems. These themes are explored at multiple scales, from the watershed to the stream reach, in three core chapters. I first evaluate the challenges and opportunities of monitoring intermittent streams in Chapter 1, before moving to understanding the controls on wetted channel extent and variability in Chapter 2, to finally characterizing the shifting habitat mosaic in Chapter 3. These three chapters together illustrate the importance of intermittent streams in shaping the environments they flow (and cease to flow) through, and underscore the need to capture the patterns of drying across space and time.
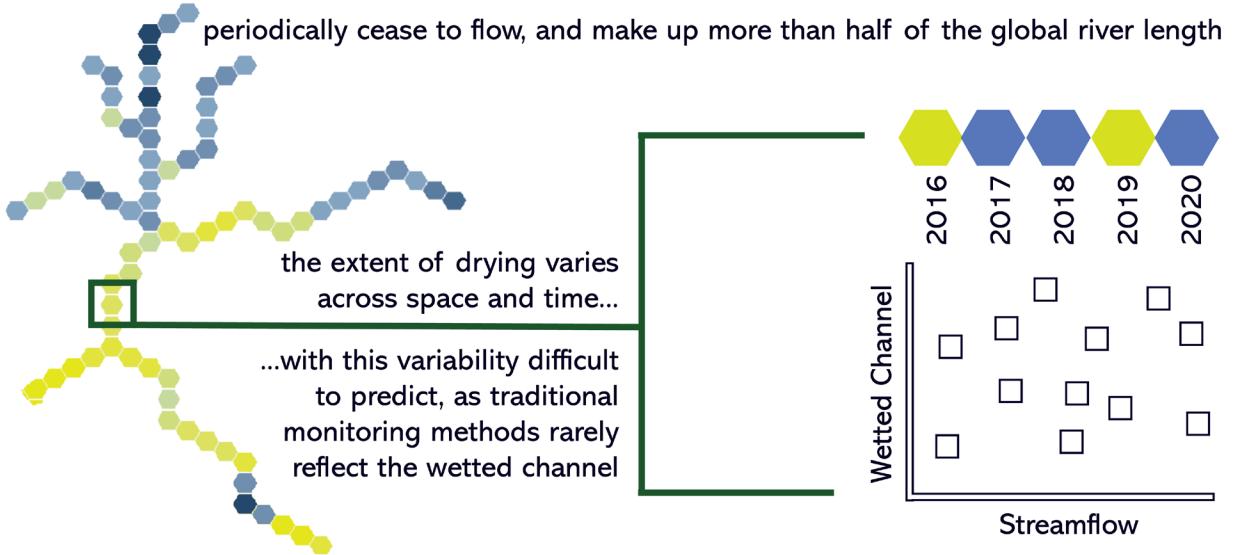
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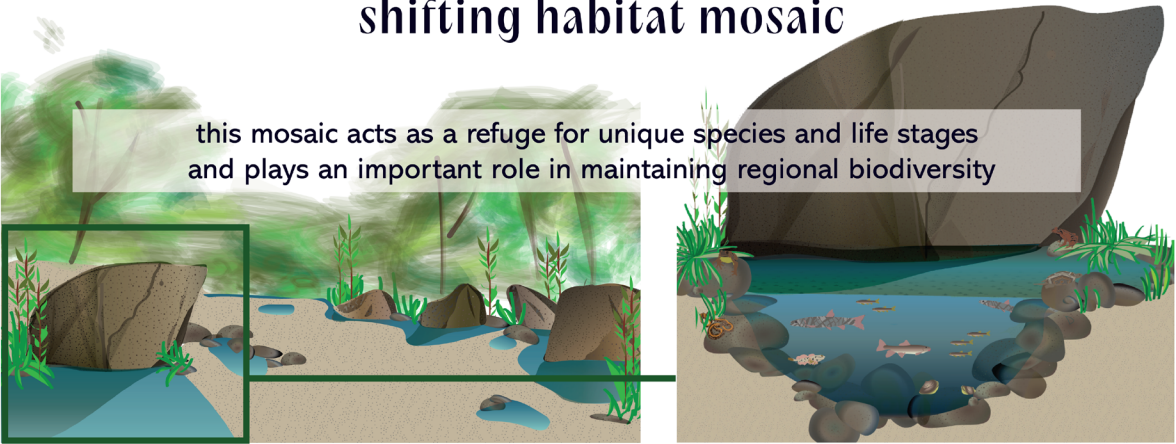
INTERMITTENT RIVERS

periodically cease to flow, and make up more than half of the global river length

the extent of drying varies across space and time...

...with this variability difficult to predict, as traditional monitoring methods rarely reflect the wetted channel

2016 2017 2018 2019 2020

Wetted Channel

Streamflow

the spatial and temporal patterns of drying are largely controlled by

geology   meteorology   land cover

and these factors come together to create a heterogeneous riverscape, moving between flowing reaches, isolated wet patches, and dry channels - that collectively form a

shifting habitat mosaic

this mosaic acts as a refuge for unique species and life stages and plays an important role in maintaining regional biodiversity

my work focuses on the hydrological and ecological patterns within intermittent stream systems, to understand the controls and consequences of variability in the wetted channel

INTRODUCTION

Intermittent streams, characterized by a cessation of flow during dry periods (Boulton et al., 2017), are widespread across the world and make up a large proportion of the stream network in many regions (Messager et al., 2021). Largely understudied and underappreciated compared to their perennial counterparts, these systems support rich and unique biological communities (Meyer et al., 2007), with several native taxa that are adapted to the temporary characteristic of these waterways (Stubbington et al., 2017; Kerezsy et al., 2017). Further, intermittent streams provide important ecosystem services (Koundouri et al., 2017; Pastor et al., 2022), including water provision, flood control, and support of downstream water quality and productivity (Biggs et al., 2017). Despite their ubiquity and environmental importance, intermittent streams remain vulnerable to a myriad of threats, including altered climate regimes (Larned et al., 2010), increased anthropogenic disturbance (Chiu et al., 2017), and changing regulatory protections (Keiser et al., 2022). Given these threats, an improved understanding of intermittent stream dynamics and their role in supporting biodiversity and ecosystem resilience is required (Lane et al. 2022).

Stream drying and contraction within intermittent streams is highly dynamic, where the wetted habitat quantity can decrease by large proportions by the end of the dry season (Stanley et al., 1997; Jensen et al., 2019) and can be variable year-to-year (Allen et al., 2019; Lapides et al., 2021; Moidu et al., 2021). Whether a channel begins to disconnect from the headwaters, mid-reaches, or downstream (Lake, 2003), fragmentation creates a series of habitat patches of varying persistence and isolation (Datry et al., 2017). This leads to a heterogeneous riverscape, moving between flowing reaches, isolated wet patches, and dry channels that collectively form a shifting habitat mosaic (Datry et al. 2014). While the initial fragmentation of intermittent streams can be predictable, the onset, duration, and degree of contraction often is not (Williams, 2006), suggesting considerable potential for variation in habitat quantity, quality, and connectivity over time. This dynamism is expected to be most pronounced in systems with variable climate regimes, such as those found in Mediterranean-climate regions, including the Mediterranean Basin and parts of California, South Africa, Australia, and Chile. These climate regions have characteristic seasonality in precipitation (Gasith & Resh, 1999; Deitch et al., 2017), with wet winters followed by dry summers, as well as distinctively high variability in total precipitation across years. This inter- and intra-annual variation leads to differences in the wetted channel extent both within and across years, with likely consequences for species distributions, nutrient cycling, and water resource management.

While climate variability plays a critical role in regional spatial and temporal patterns of the wetted channel, geologic and land cover conditions act as important controls at localized scales (Costigan et al., 2016). In some cases, distinct subsurface or near-surface properties can either amplify or diminish antecedent precipitation. Recent work has shown that water held within weathered bedrock can contain significant proportions of annual rainfall, thus regulating the timing of streamflow (Rempe & Dietrich, 2018) and extent of the wetted channel (Lovill et al., 2018). Hahm et al. (2019) similarly found that certain geologic characteristics can effectively

decouple regions from precipitation volatility, and subsurface storage characteristics can work to buffer regions from anomalous climatic conditions. This interplay between long term climate patterns and the highly localized influence of the underlying physical structure results in a heterogeneous wetted channel response. While the general controls on intermittency are known, there are few studies that have evaluated the spatial patterning of the wetted channel across years.

Such variability in distribution of wetted habitat is particularly consequential for aquatic biota. As a stream contracts, remnant surface water acts as a refuge for many species, where individuals can initially benefit from certain local attributes such as concentrated prey (Rossi et al., 2022) or a lack of competitors (Erman & Hawthorne, 1967). However, as stream drying intensifies, aquatic species face increasingly stressful conditions, and the spatial and temporal arrangement of such refuges become critical in determining species survival (Magoulick & Kobza, 2003). The direct impacts, such as habitat loss, and indirect impacts, such as deteriorating water quality, of stream drying can have significant and lasting ecological implications, including altered population abundances, trophic structure, and species interactions (Lake, 2003). Many aquatic organisms in regions prone to seasonal drying have developed resistance and resilience strategies to overcome periodic channel contraction, such as tolerance to hypoxia or hyperthermia (Matthews, 1987; Labbe & Fausch, 2000), movement into the hyporheic zone (Stubbington, 2012; Rodriguez-Lozano et al., 2019), or dispersal to wet reaches (Davey & Kelly, 2007; Bogan et al., 2017). However, the success of such behavioral and physiological adaptations is highly dependent on the extent and connectivity of remnant habitat patches (Sarremejane et al., 2021), which can be highly variable both within and across years (Costigan et al., 2017). Further, changing climate regimes are predicted to have an increased frequency of long-term, supra-seasonal droughts. These extreme disturbance events are unpredictable in their magnitude and duration, and recovery from such conditions through resistance and resilience strategies is much more variable than recovery from seasonal disturbances (Lake, 2003; Bogan et al., 2014). Given that species can exhibit differential responses to disturbance based on spatiotemporal habitat characteristics (Liao et al., 2017), determining the mechanisms that underpin wetted channel variability, and in turn, how species respond to such heterogeneity across time, can shed light on how these dynamic systems can support ecosystems and communities under a changing climate.

Intermittent streams are especially sensitive to climate fluctuations and, compared to perennial streams, are predicted to be the most at risk of hydrologic regime shifts (Dhungel et al., 2016). Yet, relatively little attention has been given to documenting and evaluating the factors that influence variability in intermittent stream drying. Without documenting how intermittent streams vary within and across years, an essential component of their character is lost. With projections for more volatile climate conditions (Portner et al., 2022), there is considerable potential for intermittent stream ecosystems, and the species and services they support, to shift in response. Understanding where viable wetted habitat exists within a river network is a key management concern, but existing tools are often based on static conditions. Tonkin et al. (2019) recently called for novel strategies that approach river ecosystem work with a focus incorporating increasing climatic variability. My work addresses this challenge by exploring the environmental consequences of intermittent stream variability, and focuses on the interannual variation in the hydrological and ecological patterns of intermittent streams. These themes are explored at

multiple scales, from the watershed to the stream reach, in three core chapters of this dissertation. I first explore inter- and intra-annual intermittent stream patterns, before moving to determining the controls on both the extent and variability of the wetted habitat. Finally, I evaluate the ecological consequences of intermittent stream dynamics, using a novel approach considering intermittent streams as shifting habitat mosaics.

In Chapter 1, I document wetted channel patterns and evaluate the ability of traditional monitoring methods to capture wetted channel variability across space and time. While recognition of the importance of intermittent systems has grown in recent years, little is understood about the drying dynamics within the channel, and the implications this variability has on the ecology, hydrology, and management of their watersheds. Monitoring methods that are spatially and temporally explicit are required to understand how variability in the degree and extent of drying impacts the functioning of these systems (Zimmer et al., 2020). However, traditional monitoring methods are typically not suitable for capturing the dynamism of intermittent systems across space and time (Borg Galea et al., 2019). Stream gauges are one of the most common monitoring tools, but only provide information at a discrete point location, suffer from placement bias, and tend to under-represent intermittent streams (Costigan et al., 2017; Krabbenhoft et al., 2022). Given its wide usage, a question arises over whether streamflow records reflect intermittent conditions within systems more broadly, and how the two can be leveraged to improve and target monitoring efforts. By comparing the mapped wetted channel with hydrologic gauge readings, I evaluated the relationship between the two across years at four sites: Rio Grande in New Mexico, San Pedro River in Arizona, Russian River watershed in Northern California, and Coyote Creek in Central California. Results showed that gauge readings reflected wetted channel conditions to varying degrees. In many cases, gauges recorded zero-flow readings despite wet reaches both upstream and downstream of the gauge, while some gauges consistently recorded non-zero-flow readings despite dry reaches both upstream and downstream of the gauge. In contrast, some sites exhibited a strong relationship between streamflow and wetted channel conditions, with these sites tending to be located in areas with minimally altered watersheds. I found that wetted channel mapping can be used to complement streamflow gauge readings during low flow conditions, when drying thresholds are surpassed or during high rates of anthropogenic streamflow alteration. Knowing where and when streams dry is critical for managing ecosystems and water resources, and complementing streamflow gauge records with a spatially explicit surveying method, such as through wet-dry mapping, remote sensing, or sensor arrays, is recommended for future monitoring campaigns.

Chapter 2 expands on the patterns of wetted channel response described in Chapter 1, but looks more closely at the mechanisms and controls driving the extent and variability of drying. The degree of stream drying can vary greatly across space and time depending on both landscape features and antecedent precipitation conditions (Costigan et al., 2017). Yet, the factors that influence interannual variation in intermittent stream drying remain poorly understood. With increasing precipitation volatility and rising temperatures (Swain et al., 2018), there is an urgent need to characterize where and when intermittent streams will be buffered from, or vulnerable to, climate change, with ultimate implications for hydrology and freshwater ecology. Focusing on the Russian River watershed in California, I combined field observations of wetted channel

extent with land cover, physiographic, and climate variables to develop two models that predict the degree and variability of drying along the wetted channel. Both models were then applied across the watershed to predict the stability of intermittent conditions throughout the entire network. With this, I characterized streams based on their sensitivity to climate variability and identified stream reaches predicted to be reliably dry, those responsive to antecedent precipitation, and those predicted to be reliably wet and buffered from climate variability. Climatic variables largely controlled the extent of the wetted network at the end of the season, with an emphasis on long term precipitation, pointing to the importance of hydrologic memory. The degree to which hydrologic memory contributed to the condition of a reach was dependent on the underlying physical structure, with regions underlain by sedimentary rock tending to amplify hydrologic memory, while regions underlain by metamorphic rock tending to diminish hydrologic memory. The ability to predict where the wetted channel will persist through the dry season is critically important for sustaining aquatic biodiversity in arid and semi-arid regions, a thread I develop further in Chapter 3.

In Chapter 3, I explore how the variability in intermittent stream conditions supports aquatic and semi-aquatic species across time. The high degree of inter- and intra-annual variation in the wetted channel that I document in previous chapters leads to differences in the availability of habitat types within and across years, with consequences for species distribution, habitat partitioning among species and life stages, and recruitment variability. Given that intermittent streamflow conditions are projected to become increasingly severe (Larned et al., 2010; Pumo et al., 2016; Zipper et al., 2021), often coinciding with critical periods of species' life history (Jaeger et al., 2014), an improved understanding of species' responses to wetted habitat variability within intermittent streams is needed. Further, new insights into intermittent stream ecology can be gained by approaching intermittent streams as shifting habitat mosaics that vary both within and across years. In this chapter, I characterize the habitat mosaic in Coyote Creek, California, and evaluate its role as a refuge for native and imperiled species. I combined wetted habitat and vertebrate abundance surveys during the dry season from seven years, spanning both extreme wet and extreme dry annual precipitation conditions, and characterized variation in the size, persistence, and spatial configuration of wetted habitats in relation to the observed abundance and composition of aquatic and semi-aquatic vertebrates. I found that some wetted habitats persisted across all years, regardless of antecedent precipitation, whereas others dried in all but the wettest years. I determined that persistent pools, a subset of wetted habitats present in the stream, support a diverse assemblage of native species even during extreme dry conditions, while transient pools act as important habitat for particular species and life stages. These results suggest that intermittent streams can be characterized as shifting habitat mosaics that support unique species and life stages across space and time and play an important role in maintaining regional aquatic biodiversity.

Together, my work focuses on the hydrological and ecological patterns within intermittent stream systems to understand the controls and consequences of variability in the wetted channel. Interest in intermittent streams has been growing rapidly in recent years, with increased recognition of their role in supporting ecosystem services and biodiversity. My work shows that traditional and widespread stream gauging methods are inadequate in recording the variability of

intermittent streams, and that relying on these stationary measures puts us at risk of systematically mischaracterizing these systems. My research also demonstrates that it is possible to model wetted channel dynamics in intermittent streams. Such models not only provide insights into the various physiographic and climatic controls on wetted channel conditions, but also enable the prediction of the extent and variability of drying under different climate conditions. The modeling approach I developed also makes it possible to distinguish between persistent wetted reaches, that retain the signal of long-term precipitation and are buffered from fluctuating climate, and reaches that are more responsive to antecedent precipitation conditions, leading to variability in the available wetted habitat for aquatic species. Finally, by considering intermittent streams as shifting habitat mosaics, my research reveals three main typologies of over-summer habitat based on hydrologic quantity, quality, and connectivity: 'transient, small' and 'transient, large' habitat units that are sensitive to antecedent rainfall, and 'persistent, large' habitat units that are reliably wetted even through the driest conditions. These typologies correspond to unique biotic assemblages, particularly between large, isolated but persistent habitat units versus small, closely-linked patches. Large, persistent habitat units sustain populations of adult fish that are rarely found in shallow habitat units, and act as the only refuge for all species during severe dry conditions. If these persistent habitat units become the only aquatic habitat during the dry portions of every year, species will face increasingly limited and stressful conditions in these few remaining habitat units.

My work establishes the importance of considering variability in intermittent stream dynamics, and punctuates the need for future work to capture how this variability affects long-term environmental processes. Given projections for increased climate volatility and extreme conditions, special consideration must be given to intermittent stream systems, which support unique hydrologic and ecologic functions. My work addresses this directly, from evaluating the challenges of monitoring intermittent streams in Chapter 1, to understanding the controls on wetted channel extent and variability in Chapter 2, to characterizing the ecological consequences of the shifting habitat mosaic in Chapter 3. These chapters collectively underscore the value of wet-dry mapping in characterizing the hydrological and ecological dynamics of intermittent streams. Variability across space and time is a fundamental aspect of intermittent streams, and capturing this through spatially explicit approaches is required to expand on our understanding of these systems.

CHAPTER 1 | on the relationship between streamflow and the wetted channel

Abstract

Channel drying is a phenomenon characteristic to intermittent streams. The timing, magnitude, and frequency of drying can be highly variable both within and across years. Due to this, monitoring intermittent streams using traditional stationary methods, such as streamflow gauges, are typically inadequate in capturing the dynamism of these systems. Streamflow records allow us to track conditions over time, but are limited to a single point in space, while wetted channel surveys offer a spatial understanding of the stream channel, but are limited to a snapshot in time. In this study, we assess how these two complementary monitoring methods can be coupled to capture the spatial-temporal dynamics of drying within intermittent streams. Using a subset of wetted channel mapping sites with at least 5 years of survey data and paired streamflow gauge data, we explore how the patterns and extent of wetted channels corresponded to gauge readings using correlation, logistic regression, and coefficient of variation metrics. Then, for streams with repeated wet-dry mapping and multiple nested gages, we identified locations where gage readings most strongly correlated with wetted conditions and explored the site-specific factors that influenced the relationship between at-a-station flow measurements and reach-scale wetted channel extent. We found that sites with the strongest relationship between wetted channel conditions and streamflow readings were located in areas with minimally altered watersheds. At other sites, we found little correspondence between stationary streamflow gauge readings and wetted channel dynamics near the gauge. In some cases, gauges reported zero-flow readings despite wet reaches both upstream and downstream of the gauge, while in others, the gauges consistently had non-zero-flow readings despite dry reaches both upstream and downstream of the gauge. In many cases, we found that streamflow gauges acted as an indicator or proxy for wetted channel extent until a certain low flow threshold, after which wetted channel surveys were more informative of conditions. Overall, this work shows how wetted channel surveys and streamflow gauge data can be combined and leveraged to better understand intermittent stream dynamism and develop recommendations for improved monitoring of intermittent systems.

Introduction

Intermittent streams represent much of the global river network (Messager et al., 2021), and are characterized by a lack of flow during dry periods (Datry et al., 2016). While channel drying is a common and natural phenomenon, intermittent streams can exhibit markedly different drying regimes (Price et al., 2021), varying greatly in the timing, duration, and spatial extent of flow cessation. This heterogeneity in drying dynamics ultimately has implications for the hydrological, biogeochemical, and ecological functioning of a watershed (Levick et al., 2008). For example, the degree and duration of drying can determine available refuge habitat for species (Bogan et al., 2019), impact nutrient pulses (Datry et al., 2018a), and influence various ecosystem services and functions (Datry et al., 2018b), including water provision, flood control, and support of downstream water quality and productivity (Biggs et al., 2017).

While recognition of the importance of intermittent systems has grown, challenges remain in characterizing the dynamic patterns of drying that occur within intermittent stream channels (Shanafield et al., 2021). Monitoring methods that are spatially and temporally explicit are required in order to understand how variability in the degree and extent of drying impacts the functioning of these systems (Zimmer et al., 2020). However, traditional monitoring methods such as streamflow gauges are often not suitable for capturing the dynamism of intermittent systems across space and time (Borg Galea et al., 2019; Falcone et al., 2010). Stream gauges are one of the most widespread stream monitoring tools, but there is substantial uncertainty in estimating zero- or low-flow conditions (Zimmer et al., 2020). Furthermore, gauges only capture flow conditions at a discrete point location, which may not represent conditions in the stream channel upstream and downstream of the gauge. Alternative monitoring methods are needed to measure the spatial patterns of drying in intermittent streams.

One such method is wetted channel mapping surveys, used to document the spatial extent of surface water conditions at a moment in time (Costigan et al., 2017). Studies using wetted channel mapping have greatly increased our understanding of intermittent stream dynamics. For example, in ecological research (Allen et al., 2019; Woelfle-Erskine, et al., 2017; Archdeacon et al., 2022), wetted channel mapping has elucidated how the persistence and survival of aquatic species may be limited by the degree and distribution of drying. Wetted channel mapping has also been employed to understand physical controls of stream drying (Jensen et al., 2014; Godsey & Kirchner, 2014; Lovill et al., 2018), shedding light on how lithology, geomorphology, of near-surface properties can influence the expansion and contraction of the wetted extent. Further, such surveys have been successfully used to model and predict spatial patterns of intermittent stream dynamics (Ward et al., 2018; Yu et al., 2019; Moidu et al., 2021).

Despite the growing use of wetted channel mapping in intermittent stream research, there are notable limitations. The method is resource-intensive, requiring that personnel directly survey

the stream channel, and can be difficult to implement at high frequencies, over broad spatial scales, and in areas with access constraints (Costigan et al., 2017). As a result, wetted channel surveys are often limited to relatively short channel reaches and periods of time. Given the growing research interest in intermittent streams (Leigh et al., 2016), a critical evaluation of the distinct and complementary advantages and limitations of stream gauging and wetted habitat mapping is warranted. Further, understanding the congruence between these two monitoring methods can allow us to make inferences on both the temporal and spatial variability of the wetted channel.

Here, we perform the first assessment of wetted channel surveys coupled with stream gauge data to explore their relationships and utility in capturing the spatial-temporal dynamics of intermittent streams. First, we systematically searched for where wetted channel surveys have been conducted on intermittent streams in the U.S., and under what conditions wetted channel mapping is used in lieu of, or in conjunction with, stream gauge monitoring. Second, we selected a subset of wetted channel mapping sites with at least 5 years of survey data and paired streamflow gauge data to explore how the patterns and extent of wetted channels corresponded to gauge readings. Third, for streams with repeated wet-dry mapping and multiple nested gages, we identified locations where gage readings most strongly correlated with wetted conditions and explored the site-specific factors that influenced the relationship between at-a-station flow measurements and reach-scale wetted channel extent. Overall, we predict that (1) the wetted channel will largely be decoupled from streamflow, with the variability and extent of the wetted channel largely controlled by site-specific factors, and (2) we expect this decoupling to be strongest in regions with high in-stream or watershed-wide anthropogenic alteration. Through these objectives and predictions, we elucidate how wetted channel surveys and streamflow gauge data can be combined and leveraged to better understand intermittent stream dynamism, and develop recommendations for improved monitoring of intermittent systems.

Methods

Identification and motivation of wetted channel mapping datasets

We conducted a review to identify wetted channel data through literature searches, and contacting relevant watershed management, conservation agencies, and academic research groups. We used the following search terms for our literature review on Web of Science in August, 2020: {(("wetted channel*" OR "wet dry*" OR "wet-dry*") AND map*) AND (intermittent OR temporary OR non-perennial) AND (stream OR river OR channel)}, and reviewed the resulting items. We solicited additional datasets from organizations and academic groups that conduct wetted channel mapping, identified through literature reviews, web searches, and social media calls for datasets. Groups and agencies contacted include The Nature Conservancy, United States Bureau of Reclamation, Russian River Salmon and Steelhead Monitoring Program, Salmon Creek Watershed Council, Southern California Coastal Water

Research Project, Dry Rivers Research Coordination Network, and the Reynolds Creek Critical Zone Observatory. We focused on wetted channel datasets from intermittent streams in the contiguous US that were mapped over continuous reaches (i.e., not spot measurements). We then assessed each site for the presence of streamflow gauges along the channel, either from USGS gauges located along the channel or from independent gauges operated by conservation and management authorities. To understand the conditions for using wetted channel mapping in lieu of or in conjunction with other monitoring methods, we assessed the motivation, or purpose, for conducting wetted channel surveys through the corresponding literature available for each site.

Relating streamflow and wetted channel conditions

We selected a subset of sites from our review with at least 5 years of surveys on record and at least one corresponding streamflow gauge for further spatial and temporal analysis. To determine the relationship between gauge readings and wetted channel conditions, we compared the proportion of the channel that was wetted upstream and downstream to the gauge reading at the time of the survey. We related gauge readings to channel conditions at two different spatial scales based on drainage area differences, i.e. 20% and 50% of the drainage area of the gauge in both the upstream and downstream direction (Figure 1).
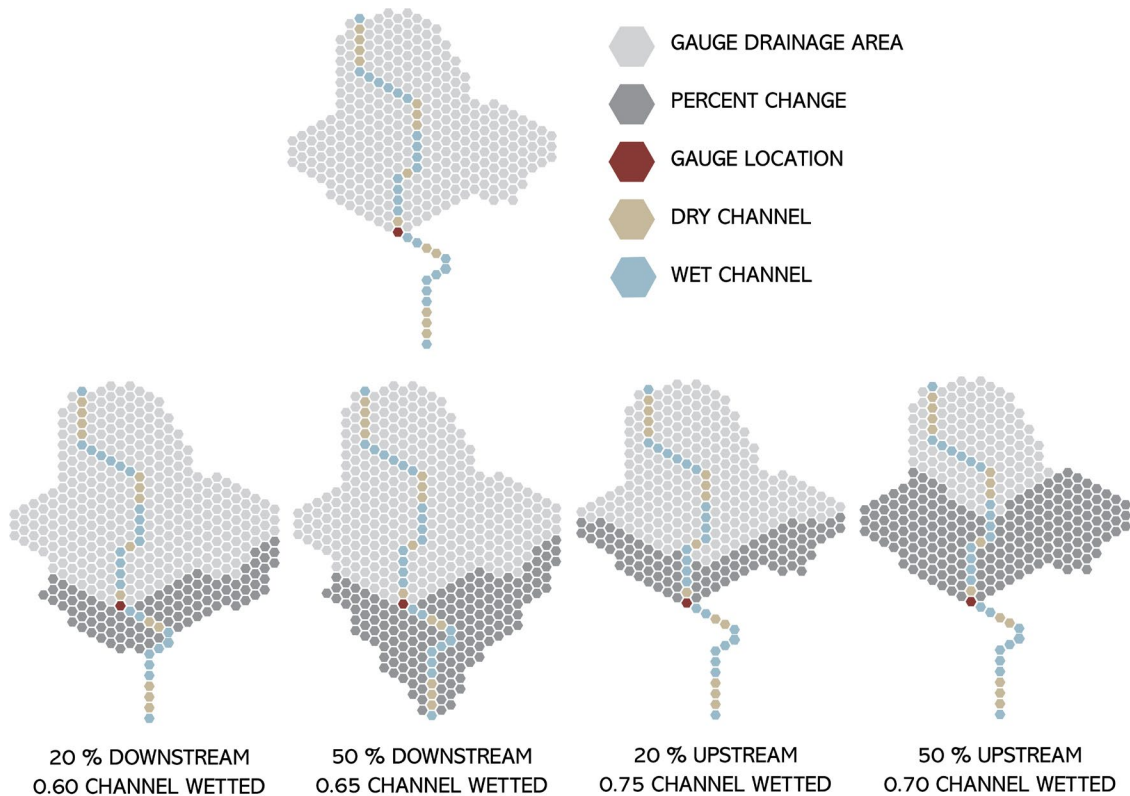

Figure 1. A subset of wetted channel conditions (within 20% and 50% of the gauge drainage area in both the upstream and downstream direction) were related to each gauge reading at the date of wetted channel surveying

We related measurements of wetted-channel extent to streamflow data using correlation, regression, coefficient of variation, and time lag analysis. To assess correlation, Spearman correlation coefficients were calculated for the proportion channel wetted and streamflow readings, where values closer to -1 and 1 indicate higher correlation and values closer to 0 indicate weaker correlation. We used logistic regressions under a generalized linear model framework to determine the regression coefficient (β) and McFadden pseudo-R^2 statistic between the proportion channel wetted and streamflow readings at each gauge. Positive regression coefficients indicate that the greater the streamflow, the greater the probability that the surveyed reach is wetted. Coefficients of variation (CV) of the proportion channel wetted during a zero-flow gauge reading were calculated to understand the variability in wetted channel extent when a streamflow gauge reported zero-flow values. Greater CV values indicate a higher variability in the proportion of the channel that remained wetted when the gauge had a zero-flow reading at the time of the survey. To determine whether wetted channel conditions exhibited a delayed response to streamflow, we assessed the Spearman correlation coefficient, logistic regression coefficient, and McFadden pseudo-R^2 between the proportion channel wetted and mean antecedent streamflow for the 7 days, 14 days, and 30 days preceding the wetted channel sampling date.

Impacts to streamflow and wetted channel relationships

Many sites included in this study contain multiple, nested gauges along the mapped channel. In these cases, we also explored differences in the correlations between gauge readings and wetted conditions, and explored the site-specific physical, land cover, and water use characteristics that could explain them. Physical characteristics were extracted from nationally available geospatial layers, including geologic coverage, obtained from the State Geologic Map Compilation (Horton, 2017) and slope, obtained from the National Elevation Database. Land use and land cover data was obtained from the National Land Cover Database (Homer et al., 2012). Water use was determined by identifying water management infrastructure, such as dams or pumping stations, as well as evidence of residential or agricultural diversions using available literature, technical documents, and watershed management plans for each site. All geospatial variables were compiled locally (dominant class or mean value from a 10 m buffer at each gauge location) and at the watershed level (contributing area of each class for each gauge drainage area) to determine at what scale these variables may influence streamflow and wetted channel relationships.

Results

Distribution and motivation for wetted channel mapping

We found twelve wetted channel datasets from intermittent streams across the US, summarized in Table 1. All of the datasets included surveys during low flow conditions following seasonal

dry-down, while some included additional surveys across a range of seasonal flow conditions. The longest-running time series of wetted channel mapping surveys was conducted by The Nature Conservancy in the San Pedro watershed in Arizona, in which 163 kilometers of stream channel, on average, have been surveyed each year since 1999. The largest spatial extent of wetted channel mapping are the 293 kilometer surveys of streams on Santa Rosa Island in California by Power & Rudolph (2018), conducted in 2014, 2016, and 2017. Overall, seven of the twelve sites were located in California, and only two were located east of the Continental Divide. Seven of the twelve mapped wetted channel sites had a corresponding stream gauge for at least one site, two used nearby reference gauges to estimate streamflow (OC, SR), and three did not have any corresponding streamflow gauge data (SC, RC, SRI).

The motivation for conducting wetted channel mapping varied across sites (Table 1), but all corresponding literature discussed the value of using wetted channel mapping to understand the spatial relationships of drying in dynamic systems. Seven of the twelve sites (SP, RG, RR, CC, OC, SRI, SC) conducted wetted channel mapping to understand the influence of drying on habitat, persistence, and/or survival of aquatic species, while two of these sites (SP, SRI) also considered impacts to riparian habitat. The remaining five of the twelve sites (ER, SN, RC, AH, SR) aimed to understand and identify the lithologic, geomorphic, and/or hydrologic controls on wetted channel extent.

Table 1. Summary and motivation of wetted channel surveys

Corresponding Literature	Watershed / Region	Site	Number of Gauges	Years Surveyed	Average Length Surveyed (km)	Motivation for wetted channel mapping
Turner & Richter 2011 The Nature Conservancy	San Pedro River, AZ (SP)	Aravaipa Creek	1	22 (1999-2021)	27	Better understand and manage riparian and aquatic habitats during low flow conditions
		Babocomari River	1		7	
		San Pedro River	3		80	
McKenna, 2019 Bureau of Reclamation	Rio Grande, NM (RG)	Rio Grande	3	14 (2007-2021)	104	Facilitate coordination among water management entities to prevent unexpected drying, slow rate of drying to alleviate negative impacts on threatened/endangered fish species
Moidu et al., 2021 Russian River Salmon and Steelhead Monitoring Program	Russian River, CA (RR)	Dutch Bill Creek	3	7 (2012-2019)	9.5	Identifying critical habitat for *Oncorhynchus kisutch* (coho salmon) and *O. mykiss* (steelhead trout), evaluating flow conditions for juvenile coho and steelhead, inform fish rescue and relocation efforts
		Mill Creek	3		14.5	
Moidu et al., (under review)	Coyote Creek, CA (CC)	Coyote Creek	1	6 (2015-2029, 2021)	5	Identify drying patterns and understand how drying affects long term species distribution and abundance
Hwan & Carlson, 2016	Olema Creek, CA (OC)	John West Fork	0 [†]	4 (2009-2012)	0.45	Estimating hydrological connectivity and patterns of stream fragmentation with ecological implications

Lovill et al. 2018	*Eel River, CA* (**ER**)	*Elder Creek*	1	4 (2012-2015)	34.02	Understanding lithologic and near-surface physical controls on wetted channel extent
		Fox Creek	0	4 (2012-2015)	5.74	
Godsey & Kirchner, 2014	*Sierra Nevada, CA* (**SN**)	*Bull Creek*	1	3 (2006-2008)	8.36	Understanding the expansion and contraction of flowing networks across topographical, geological, and climate settings
		Caspar Creek	1		14	
		Providence/ Duff Creek	1		7.81	
		Sagehen Creek	1		35.2	
Power & Rudolph, 2018	*Santa Rosa Island, CA* (**SRI**)	*Santa Rosa Island, CA*	0	3 (2014, 2016, 2017)	293	Quantifying surface water extent to understand implications for plant and animal life
Woelfle Erskine et al 2017	*Salmon Creek, CA* (**SC**)	*Fay Creek*	1	3 (2012-2014)	0.679	Evaluating over-summer survival of coho salmon and steelhead trout
		Tannery Creek	1		0.371	
Warix et al., 2021	*Reynolds Creek watershed, ID* (**RC**)	*Babbington Creek*	0	1 (2019)	2	Understanding how groundwater and topography influence stream drying
		Cottle Creek	0		1.5	
		Dryden Creek	0		5	
		Macks Creek	0		3.5	
		Murphy Creek	0		2	
		Peters Gulch	0		8	
		Reynolds Creek	0		1.5	
Jensen et al., 2014	*Appalachian Highlands* (**AH**)	*Hubbard Brook*	2	1 (2015)	8	Understanding lithologic, near-surface physical, and geomorphic controls on wetted channel extent
		Fernox Experimental Forest	3	1 (2016)	2	
		Poverty Creek	0 [†]	2 (2015, 2016)	5	
		South Fork of Potts Creek	0 [†]	2 (2015, 2016)	3	
		Coweeta Hydrologic Laboratory	3	2 (2015, 2016)	5	
Whiting & Godsey 2016	*Salmon River, ID* (**SR**)	*Cougar Creek*	0 [†]	1 (2014)	39.17	Understanding the hydrologic and geomorphic mechanisms that drive surface flow extent
		Dunce Creek	0 [†]		4.42	
		Goat Creek	0 [†]		8.31	
		Pioneer Creek	0 [†]		15.23	

[†] indicates that streamflow was estimated with reference gauges

Relating streamflow and wetted channel conditions

There were seven channels across four watersheds that fulfilled our search criteria (i.e., paired wetted channel surveys and streamflow gauge datasets spanning at least 5 years, see Methods) for further spatial and temporal analysis: Mill Creek and Dutch Bill Creek within the Russian River watershed, CA; Coyote Creek, CA; San Pedro River, Aravaipa Creek, and Babocomari River within the San Pedro River watershed, AZ; and the Rio Grande, NM (Figure 2). For one system (Russian River watershed), streamflow data was obtained from independent gauges operated by

Trout Unlimited and the Russian River Sea Grant Monitoring Program following USGS standards (Russian River Coho Water Resources Partnership, 2015). Streamflow data from all other sites were obtained from USGS-operated gauges. The duration and time period of wetted channel mapping at each of these sites was varied, as did the number of corresponding gauges (Table 1).

We compared wetted channel conditions to gauge readings at two different spatial scales, by relating gauge readings to the proportion channel wetted within 20% and 50% of the gauge drainage area (Figure 1, Table S1). We found that for most sites, the relationship between wetted channel conditions and streamflow was stronger at the 20% than the 50% drainage-area difference, with generally lower CV, higher Spearman correlation coefficients, and higher pseudo-R^2 values at the smaller scale (Table S1). In the subsequent analyses and presentation of findings, we therefore focused on the relationships between gauge readings and channel extent within the 20% drainage-area difference of the gauge.

Streamflow and wetted channel statistics for each site revealed that streamflow readings from gauges had highly variable relationships with wetted channel conditions (Figure 3; Table S1). Among all sites, Spearman correlation coefficients ranged from 0.017 - 0.92; β coefficients ranged from 0 - 7.91; R^2 from 0 - 0.76; and CV from 0.01 - 0.81. Coyote Creek, Aravaipa Creek, some sites along Dutch Bill Creek (gauge #40068), Mill Creek (gauge #160201, #160610), and Rio Grande (gauge #8355490, #8354900) showed the highest correlation between the gauge reading and wetted channel extent (0.51 - 0.92; Figure 3; Table S1). Positive β values indicate that increasing streamflow positively corresponds to a greater extent of wetted channel, with the highest values observed at Coyote Creek (7.91), and the lowest values at one San Pedro River site (gauge #9471550; 0) and all Rio Grande sites (0 - 0.03). Results show that Coyote Creek, Aravaipa Creek, and one site on Mill Creek (gauge #160610) had high pseudo-R^2 values (0.70 - 0.76) from logistic regression models, indicating a strong relationship between wetted channel conditions and streamflow. Repeated surveys from Coyote Creek indicated that this positive relationship between wetted channel conditions and streamflow was strongest during the early summer months of July and August (Figure S1), before zero-flow conditions occurred at the gauge. In contrast, during zero-flow conditions at Coyote Creek in September and October, there was a large variation in wetted channel conditions (Figure S1; Figure 3; Table S1). Many other sites also exhibited high variability in wetted channel condition at zero-flow gauge readings (Figure 3), with the greatest CV observed at San Pedro River (gauge #9471550, #9470500), Coyote Creek (gauge #11169800), and Rio Grande (gauge #8355400), ranging from 0.57 - 0.81. In contrast, there was lower CV among wetted channel conditions during zero-flow conditions at Mill Creek (gauge #160311, # 160610) and Aravaipa Creek, ranging from 0.01-0.18.
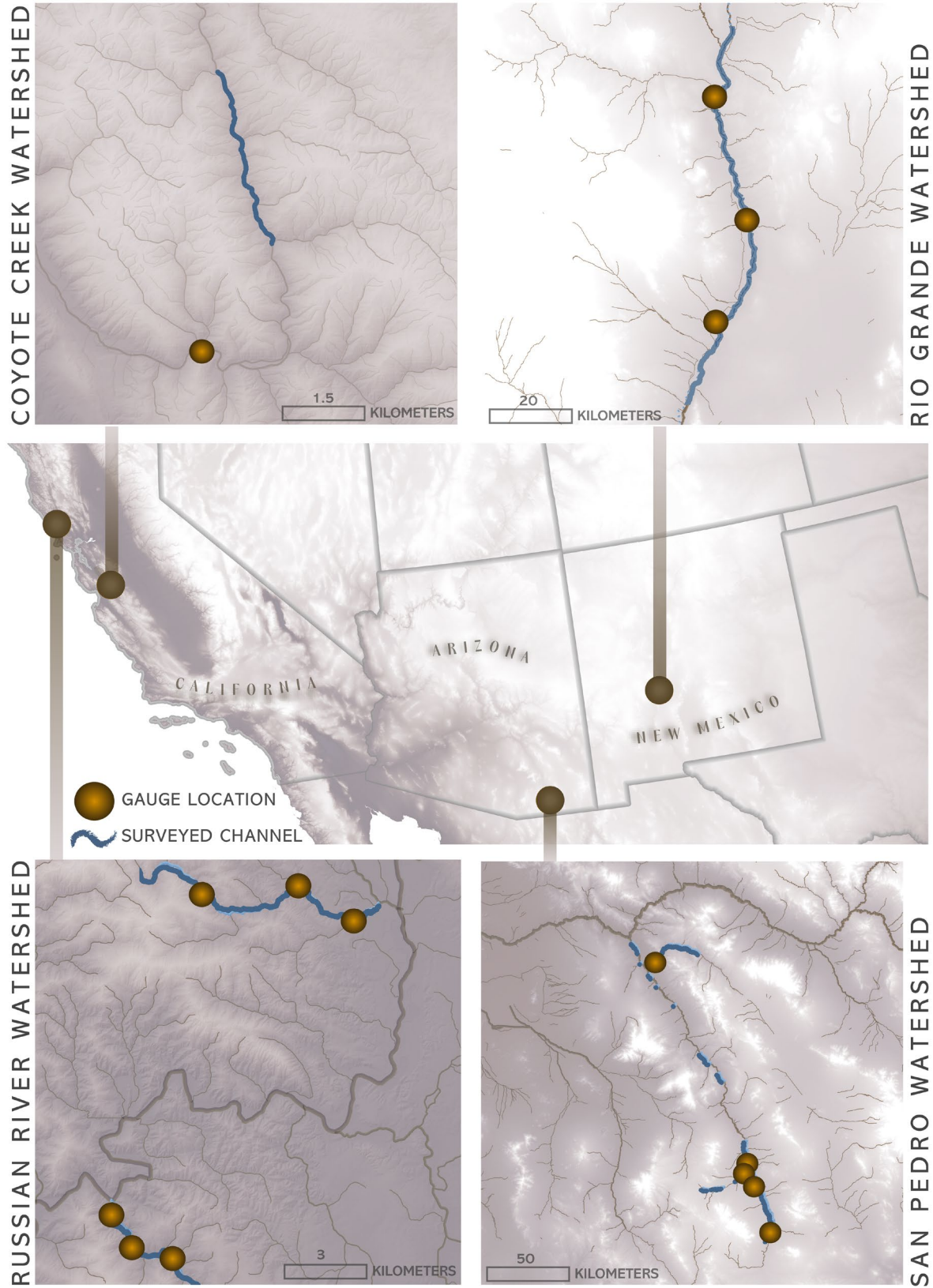
Figure 2. Distribution of sites with paired wetted channel surveys and streamflow gauge datasets spanning at least 5 years

When assessing congruency between wetted channel conditions and daily antecedent streamflow records from the preceding 7, 14, and 30 days, we observed a relationship between lagged streamflow and wetted channel extent at some sites (Table S2). For example, in terms of correlation with wetted channel extent, all sites at the San Pedro River and the Russian River had a stronger correlation with 30 day mean antecedent streamflow than shorter time lags; Coyote Creek and Babocomari River had a stronger correlation with 14 day mean antecedent streamflow than the other lags; while Aravaipa Creek had a stronger correlation with 7 day mean antecedent streamflow than longer lags (Table S2). Similar patterns were observed when considering the pseudo-R^2 between lagged streamflow and wetted channel extent, while the β coefficients were lower at all time lags and decreased with increasing lag period of streamflow.
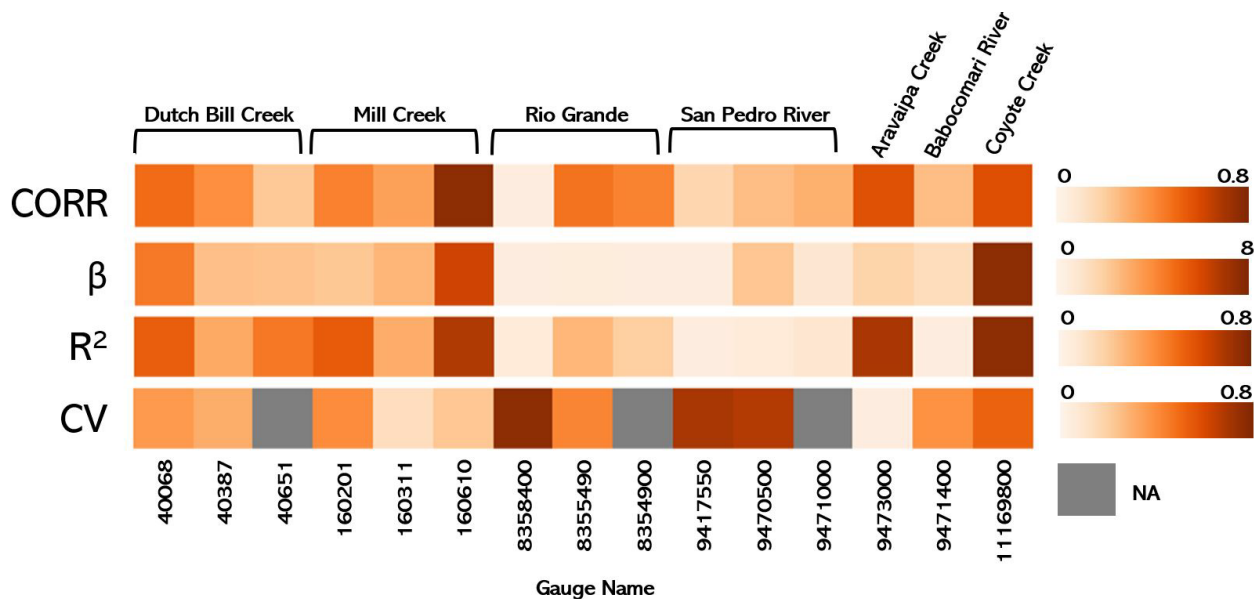

Figure 3. Relationship between the streamflow gauge readings and the extent of wetted channel within a 20% drainage-area distance from the gauge using four metrics: Spearman correlation coefficient (CORR); logistic regression coefficient (β), McFadden pseudo-R^2; and coefficient of variation (CV) for all gauge stations

Impacts to wetted channel and streamflow relationships

For sites containing multiple gauges along the mapped channel ('nested gauges'), we identified locations where gauge readings most strongly correlated with wetted conditions, and explored the site-specific physical, land cover, and water use characteristics that may influence differences in the streamflow and wetted channel relationship. At Mill Creek, gauge #160610 had a greater correlation between the proportion of the channel that remained wetted compared to the two other nested gauges along the channel (Figure 3). When comparing the land cover properties at

these sites, we see that there is a greater proportion of the upstream watershed that has natural land cover (forested, shrubland, and wetland combined), whereas the two downstream nested gauges had greater proportions of developed and agricultural land cover in the upstream watershed (Table S3). At Dutch Bill Creek, we also noted stronger relationships between streamflow and wetted channel conditions at gauge locations with a lower proportion of developed land cover in the upstream watershed (Table S3). Similarly, Aravaipa Creek and Coyote Creek have the highest proportion of natural land cover of all sites (Table S3), as well as the strongest relationship between wetted channel conditions and streamflow by pseudo-R^2 metrics, as well as high correlation coefficients (Figure 3; Table S1). These sites also have limited impacts due to their locations within protected areas.

At the San Pedro River, gauge #9471000 had a greater correlation with wetted channel conditions than the other two nested gauges (gauge #9471550 and #9470500) along the channel. Further, the other two nested gauges both had a high CV at zero-flow, whereas the streamflow readings at gauge #9471000 never recorded zero-flow during the time of surveying, despite dry channel recorded during mapping surveys in the vicinity of the gauge (Figure 3; Table S1). When considering the geologic setting of each station, we note that gauge #9471000 is located in a region dominated by volcanic geologic units, and consistently had higher streamflow readings, with wetted channel conditions remaining relatively constant upstream of the gauge regardless of flow (Figure 4). The other two nested gauges (gauge #9471550 and #9470500) were located in regions dominated by surficial deposits, and were characterized by very low flow, with the wetted channel displaying considerable variation at zero-flow readings, ranging from 0-100% wetted.

For the Rio Grande, gage #8355400 had a weaker relationship with wetted channel conditions than the other two nested gauges (gauge #8354900, #8358490), as evidenced by lower Spearman correlation coefficients and pseudo-R^2 values (Figure 3; Tabel S1), as well as greater CV during zero-flow conditions. This gauge is located between two pumping stations, with the upstream one (BDA South Boundary Pumping Station) regularly used to supplement flows during the dry season.
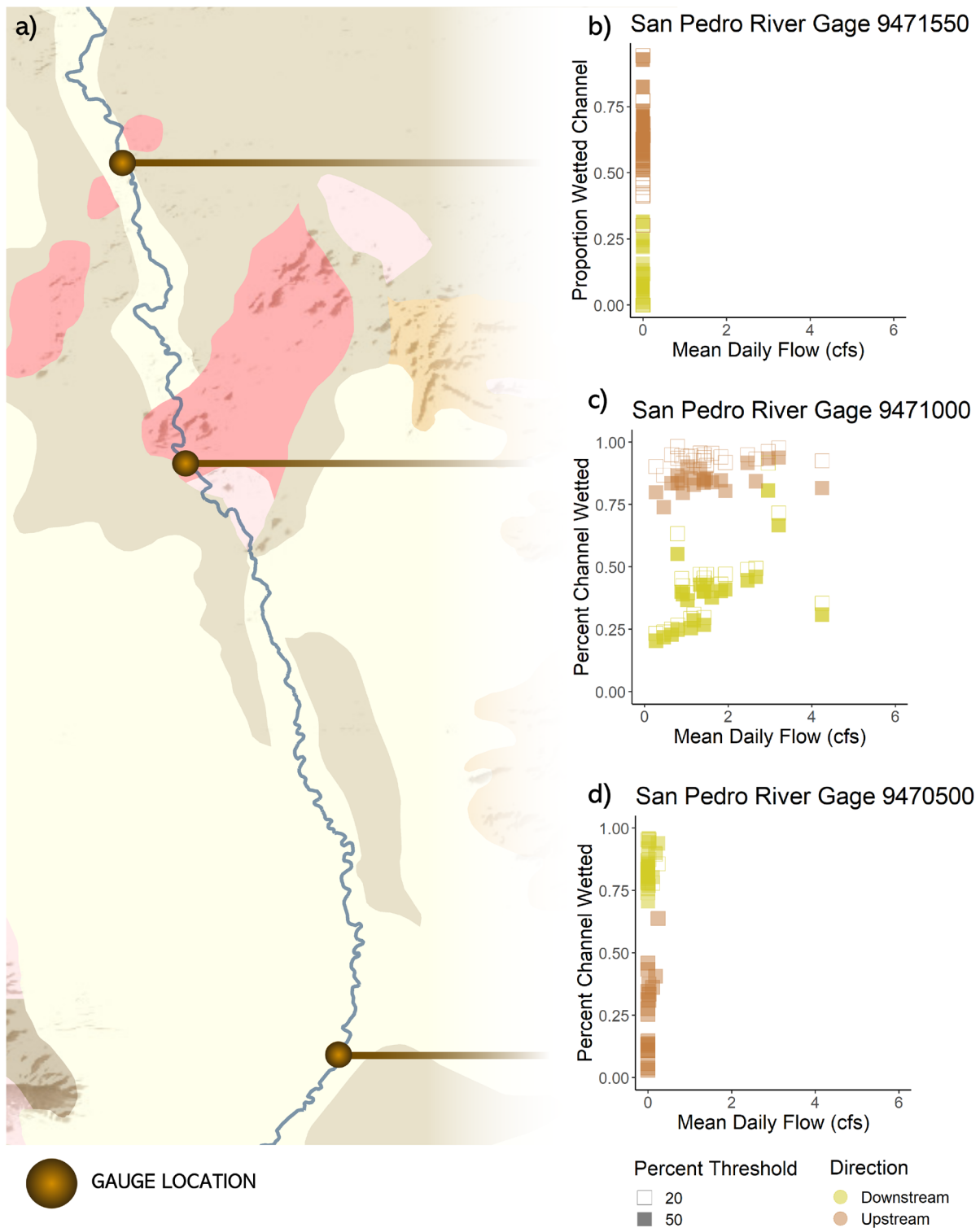
Figure 4. a) Geologic map of the San Pedro River region, AZ; Relationship between the proportion of channel that remained wetted during surveys and the mean daily flow (cfs) at the time of sampling for USGS gauge #9471550 (b), #9471000 (c), #9470500 (d)

Discussion

In this study, we explored how wetted channel mapping complements traditional stream gauging monitoring methods for characterizing intermittent stream drying dynamics. Our review found twelve wetted channel datasets across the US, mostly concentrated in the arid and semi-arid West. More than half of the wetted channel mapping was conducted to understand ecological patterns, while many others were conducted to identify physical mechanisms behind drying patterns. We selected a subset of these datasets with at least 5 years of surveys on record and at least one corresponding streamflow gauge for further spatial and temporal analysis. We observed a strong relationship between wetted channel conditions and streamflow records, with high R^2 and correlation coefficients noted at Coyote Creek, Aravaipa Creek, and Mill Creek (gauge #160610), while low CV values at zero-flow readings were observed at Aravaipa Creek and Mill Creek (gauge #160311). We found that sites with the strongest relationship between wetted channel conditions and streamflow readings were located in areas with minimally altered watersheds. However, at several other sites, we found little correspondence between stationary streamflow gauge readings and wetted channel dynamics in close proximity to the gauge. In some cases (for example, San Pedro River gage #9470500, Coyote Creek, Rio Grande gage #8355490), gauges reported zero-flow reading despite wet reaches both upstream and downstream of the gauge, while in others (San Pedro River gage #9471000) the gauges consistently had non-zero-flow readings despite dry reaches both upstream and downstream of the gauge. Overall, this work shows that wetted channel surveys provide distinct information on drying dynamics that are not captured by stream gauges.

Leveraging paired streamflow records and wetted channel mapping

Both stream gauges and wetted channel mapping provide important information regarding the dynamism of intermittent stream systems. Streamflow records allow us to track conditions over time, but are limited to a single point in space, while wetted channel surveys offer a spatial understanding of the stream channel, but typically are limited to a snapshot in time. In this study, we found that stream gauge records can be used as an indicator or proxy for wetted channel conditions under certain circumstances. For example, at many sites, we noted a relationship between wetted channel extent and mean antecedent streamflow in the preceding 7, 14, and 30 days. At sites where such a pattern is evident, future drying conditions can be anticipated, and management initiatives can be planned and adapted accordingly. For example, in the Rio Grande watershed, conservation actions such as fish rescues and flow releases to increase aquatic habitat are regularly employed (Archdeacon & Reale, 2020). These interventions are costly and labour-intensive, and the difficulty in knowing where and when such measures are needed can prohibit their effectiveness (Lawler, 2009). The ability to identify thresholds for future drying would allow conservation and water resource management to proactively conduct

wetted channel mapping to develop and target further action that focuses on mitigation, to avoid emergency measures like translocation.

Similarly, we found that streamflow records can reflect wetted channel extent until zero-flow conditions are reached, after which wetted channel surveys were more informative of conditions. At Coyote Creek, for example, the stream gauge consistently has a zero-flow reading during the late summer months of September and October, despite annual precipitation during the survey period ranging from 263 mm (2021 WY) to 1011 mm (2017 WY). This variation in annual precipitation is rather reflected in the extent of the wetted channel, which varies substantially at the end of the dry season (Figure S1). For such sites, gauge information can reflect wetted channel conditions during non-zero-flow conditions, but boots-on-the-ground surveys are needed when zero-flow conditions are reached. This understanding can limit resource-intensive wetted channel surveys to capture drying dynamics and habitat availability to when it is ecologically relevant.

Wetted channel mapping can also be employed to monitor an a priori management goal, such as flow release impacts or areas with high rates of diversion. At the Russian River watershed, streamflow gauges reflected measurable effects from instream diversions, where the cumulative effects of many small, residential diversions may cause substantial reductions in flow throughout the dry season (Russian River Coho Water Resources Partnership, 2015). At Mill Creek in the Russian River watershed, for example, initial points of disconnection occur downstream of residential clusters. The streamflow record captures this as well, where gauges with the greatest proportion of anthropogenic alteration (developed or agricultural land cover, Table S3) in the upstream watershed recorded zero-flow conditions earlier and for longer than gauges with less anthropogenic alteration upstream (Figure S2). In cases like Mill Creek, wetted channel mapping can be used when streamflows at these gauges are low or highly variable in order to understand how water diversions influence the available habitat more broadly. This example also highlights the effectiveness of seasonally deployed gauges in monitoring low flow conditions.

Implications for stream gauging

The vast majority of streams across the United States are not monitored using streamflow gauges (Falcone et al., 2010), and those that are tend to be perennial systems, with few located in headwaters or dry regions (Fekete & Vorosmarty, 2002; Krabbenhoft et al., 2022). This leads to a lack of understanding on non-perennial flow regimes, and even an underestimation of non-perennial stream systems. Further, stationary monitoring methods like stream gauges are typically not suitable for capturing the spatial dynamism of intermittent systems (Borg Galea et al., 2019), as they provide information at a discrete point location (Costigan et al., 2017), and tend to suffer from placement bias, with stations preferentially located in developed areas and low elevation reaches (DeWeber et al., 2014), leading to streamflow records affected by these

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localized conditions. For example, gauges located adjacent to residential developments or agricultural areas are at risk of capturing altered streamflow due to diversions or irrigation withdrawals (Pimentel et al., 1997; Carlisle et al., 2010; Caldwell et al., 2012). These human alterations have been shown to lead to more variable drying conditions (Hammond et al., 2021), exacerbating the uncertainty with relating streamflow records to the wetted channel. Our results indicate that the sites with the strongest relationship between wetted channel conditions and streamflow (Coyote Creek, Aravaipa Creek, and Mill Creek gauge #160610) were located in areas with the least amount of alteration upstream (Table S3). This suggests that placing gauges in largely unimpacted reaches, including nearby reference gauges, may be the best candidates for revealing the broader spatial patterns of wetted conditions in intermittent streams.

Varying the physical setting of multiple gauges along the same channel can capture variability in streamflow due to underlying geologic or land cover conditions, as seen at the San Pedro River (*section 3.3*). This has been shown in previous studies, where various streamflow metrics were highly related to the variability in specific geologic units (Tague & Grant, 2004; Lovill et al., 2018) or various landscape variables (Hammond et al., 2021) within the watershed. Further, in an analysis of drying regimes across the US, Price et al., 2021 found that land cover acted as the strongest control on no-flow conditions, and recommended further studies using sub-watershed gauging to determine local drivers of streamflow heterogeneity. We show that monitoring campaigns can take advantage of multiple, nested gauges along the same streamline by diversifying placement across varying topography, physiography, or anthropogenic alteration, to understand how streamflow may be modulated by that variable.

Improved monitoring to advance conservation, management, and policy of intermittent systems

While there is growing recognition of intermittent stream ecosystem values and services (Pastor et al., 2022) much of the tools used to monitor and manage these systems rarely consider the implications of drying (Tonkin et al., 2019; Datry et al., 2017). Understanding where and when streams lose surface flow has critical implications for the hydrology, ecology, and biochemistry of intermittent streams (Stanley et al., 1997; Acuna & Tockner, 2010; Jaeger et al., 2014; Leigh & Datry, 2016). In a review of causes and consequences of zero-flow gauge readings, Zimmer et al. (2020) cautioned against extrapolating such point-based measurements to infer broader spatial patterns without additional information. The increase in zero-flow events and no-flow duration at gauges (Zipper et al., 2021; Hammond et al., 2022) underscores the need for spatially explicit monitoring methods to provide valuable information on intermittent stream drying patterns that cannot be determined from stationary stream gauging alone. In our study, we observed three gauges included that did not record any zero-flow days (gauge #8354900, #9471000, #40651), despite corresponding wetted channel surveys identifying dry reaches both upstream and downstream of the gauge. In contrast, for the gauges that recorded zero-flow, wetted channel

mapping surveys identified important habitat refuges (e.g., remnant pools) and available surface water both upstream and downstream of gauges at all sites (Table S1). Both of these scenarios are at risk of misclassifying streams based on point-location conditions, and do not reflect the dynamic and shifting nature of these systems, with distinct ecological, management, and policy implications.

Wetted channel mapping done through the sites presented in this study have contributed to the ecological and management understanding of non-perennial systems, shedding light on patterns that streamflow gauging alone cannot capture. Work done at Coyote Creek has shown that multi-year drought conditions can cause the wetted channel to contract to a few isolated pools, which act as a refuge for a diverse assemblage of native species (Bogan et al., 2019). Similarly, in the Russian River watershed, wetted channel mapping has identified refuge pools for threatened steelhead and endangered coho at the southern end of its range (Obedzinski et al., 2018; Moidu et al., 2021) that would not have been possible using gauge readings alone. At the Rio Grande, wetted channel mapping is done during low flow conditions to identify locations for possible flow releases or fish rescues, both done to help manage the endangered Rio Grande Silvery Minnow population (Archdeacon & Reale, 2020; McKenna, 2019). Meanwhile, the San Pedro watershed has been the site of wetted channel mapping surveys for over two decades in order to understand the extent of migrating bird and endangered fish habitat (Allen et al., 2019), as well as locations that would benefit from regional recharge efforts (Lacher et al., 2014). These insights would not have been possible through streamflow gauge records alone and highlight the importance of understanding spatial variation in wetted conditions. Further, each of these sites supports unique ecological and hydrological conditions that contribute meaningfully to the broader ecosystem, underscoring the need for adequate policy and regulations to protect these systems (Nadeau & Rains, 2007; Acuna et al., 2014; Walsh & Ward, 2022).

Future of monitoring intermittent systems

As described in this study, wetted channel mapping provides an accurate, spatially explicit method for monitoring the extent of stream drying in non-perennial rivers. However, this method is very resource-intensive, as it often requires field staff or volunteers to walk several kilometers of channel length during the survey (Costigan et al., 2017). Additional challenges to this method include difficulty in accessing sites, due to land-owner access, inhospitable terrain, or high flows (Borg Galea et al., 2019). Several other approaches for capturing spatial patterns of wetted habitat availability have emerged in recent years, and also hold much potential for improving our understanding of the dynamism of intermittent systems.

Remote sensing, for example, can provide spatially explicit information on the extent of drying, and can be captured at any time depending on visibility conditions (Maswanganye et al., 2022). This method has proven successful in many catchments (Walker et al., 2019; Seaton et al., 2020;

Dralle et al., 2022), but typically requires high resolution imagery and exposed channels, although synthetic aperture radar performs well regardless of cloud cover (Palmer & Ruhi, 2018). Sensors and cameras can be deployed to passively monitor channels as well. Using an array of flow intermittency (Jensen et al., 2019) or electrical resistivity sensors (Pearson et al., 2022) along the channel can provide information on longitudinal connectivity, and is less resource-intensive than field mapping, although they do require at least two site visits to deploy and retrieve sensors. Cameras can also be deployed at locations to capture time lapse imagery of the channel (Noto et al., 2022). These latter two methods are particularly useful in monitoring known areas of interest, such as the first point of disconnection in a channel or critical habitat refuges.

While monitoring intermittent streams presents challenges not faced with perennial rivers, there are several alternatives that are able to capture the extent of drying. Knowing where and when streams dry is critical for managing ecosystems and water resources, and complementing streamflow gauge records with a spatially explicit surveying method is recommended for future monitoring campaigns.

Conclusion

Intermittent streams are characterized by spatiotemporal variability in drying, and using point-based monitoring tools, like streamflow gauges, offer limited insight into the patterns of drying, particularly during zero- and low-flow conditions. Capturing the variability of drying is critical in order to monitor these systems for ecological or management purposes. This study explores the capacity for streamflow gauges in capturing wetted channel conditions in intermittent streams. We found gauge records can reflect the degree and variability of drying to a certain extent, and can be augmented with wetted channel mapping during zero- and low-flow conditions to target and improve monitoring efforts. Knowing where and when streams dry is critical for managing ecosystems and water resources, and complementing streamflow gauge records with a spatially explicit surveying method, such as through wetted channel mapping, remote sensing, or sensor arrays, is recommended for future monitoring campaigns.

Acknowledgements

Supplementary Information

Table S1. Summary of statistics relating streamflow and wetted channel for each gauge location, based on the subset of locations with at least five years of data and a streamflow gauge. Two subsets (within 20% and 50% of the gauge drainage area in both the upstream and downstream direction) of wetted channel conditions were determined and related to gauge records separately.

Site	Gauge Name	Correlation coefficient (Spearman)		β (regression coefficient)		McFadden pseudo R²		CV of wetted channel at zero-flow	
		20%	50%	20%	50%	20%	50%	20%	50%
Dutch Bill Creek	40068 River Kilometer 0.68	0.61	0.17	4.70	1.41	0.55	0.51	0.36	0.36
	40387 River Kilometer 3.87	0.46	0.15	1.93	0.93	0.27	0.26	0.28	0.29
	40651 River Kilometer 6.51	0.20	0.20	1.82	0.10	0.46	0.46	NA (no zero-flow)	NA (no zero-flow)
Mill Creek	160201 River Kilometer 2.01	0.52	0.50	1.62	1.53	0.56	0.33	0.41	0.39
	160311 River Kilometer 3.11	0.38	0.22	2.32	2.31	0.26	0.21	0.085	0.087
	160610 River Kilometer 6.10	0.92	0.92	6.76	6.70	0.70	0.70	0.18	0.18
Coyote Creek	USGS# 11169800	0.74	0.73	7.91	7.91	0.76	0.76	0.57	0.57
Aravaipa Creek	USGS# 9473000 River Kilometer 9.50	0.73	0.88	1.14	0.40	0.71	0.65	0.01	0.03
Babocomari River	USGS# 9471400 River Kilometer 5.50	0.25	0.27	0.73	2.00	0	0	0.39	0.48
San Pedro River	USGS# 9471550 River Kilometer 154	0.13	0.04	0	0	0	0	0.76	0.54
	USGS# 9470500 River Kilometer 200	0.25	0.23	1.71	2.77	0.01	0.04	0.74	0.58
	USGS# 9471000 River Kilometer 170	0.31	0.27	0.26	0.22	0.03	0.03	NA (no zero-flow)	NA (no zero-flow)
Rio Grande	USGS# 8358400 River Kilometer 110	0.02	0.02	0.01	0	0.01	0.02	0.81	0.93
	USGS# 8355490 River Kilometer 141	0.58	0.47	0.03	0	0.22	0.09	0.44	0.58
	USGS# 8354900 River Kilometer 184	0.51	0.17	0	0	0.13	0.03	NA (no zero-flow)	NA (no zero flow)

Table S2. Relationship between proportion channel wetted and mean antecedent streamflow for 7 days, 14 days, and 30 days preceding the wetted channel survey date. Bolded values indicate the greatest value surpassing that between the proportion channel wetted and streamflow at the wetted channel survey date, i.e. with no lag (Table S1).

| Site	Gauge Name	Correlation coefficient (Spearman)			β (regression coefficient)			McFadden pseudo R²		
		Antecedent Days			*Antecedent Days*			*Antecedent Days*		
		7	*14*	*30*	*7*	*14*	*30*	*7*	*14*	*30*
Dutch Bill Creek	40068 River Kilometer 0.68	0.63	0.70	**0.72**	0.65	0.28	0.10	0.59	**0.60**	0.60
	40387 River Kilometer 3.87	0.43	0.51	**0.52**	0.28	0.13	0.05	**0.30**	0.30	0.28
	40651 River Kilometer 6.51	0.19	0.24	**0.66**	0.23	0.11	0.04	**0.47**	0.47	0.45
Mill Creek	160201 River Kilometer 2.01	0.59	0.70	**0.79**	0.28	0.13	0.06	0.64	0.66	**0.77**
	160311 River Kilometer 3.11	0.39	0.39	**0.55**	0.29	0.13	0.07	0.26	0.25	**0.30**
	160610 River Kilometer 6.10	0.92	**0.95**	0.95	0.29	0.84	1.0	0.76	0.71	**0.88**
Coyote Creek	USGS# 11169800	0.74	**0.84**	0.80	0.99	0.42	0.16	0.76	0.75	**0.78**
Aravaipa Creek	USGS# 9473000 River Kilometer 9.50	**0.77**	0.71	0.66	0.13	0.05	0.02	0.63	0.69	0.61
Babocomari River	USGS# 9471400 River Kilometer 5.50	0.46	**0.48**	0.40	0.24	0.12	0.11	0	0	**0.02**
San Pedro River	USGS# 9471550 River Kilometer 154	0.19	0.14	**0.26**	0	0	00	0	0	0
	USGS# 9470500 River Kilometer 200	0.25	0.25	**0.25**	0.23	0.06	0.02	0.01	0	**0.02**
	USGS# 9471000 River Kilometer 170	0.33	0.31	**0.38**	0.03	0.03	0.02	0.03	0.06	**0.10**
Rio Grande	USGS# 8358400 River Kilometer 110	**0.05**	0.02	0.04	0	0	0	0	0	0
	USGS# 8355490 River Kilometer 141	0.55	0.40	0.32	0.03	0	0	**0.39**	0.30	0.32
	USGS# 8354900 River Kilometer 184	0.13	0.05	0.06	0	0	0	0.01	0	0
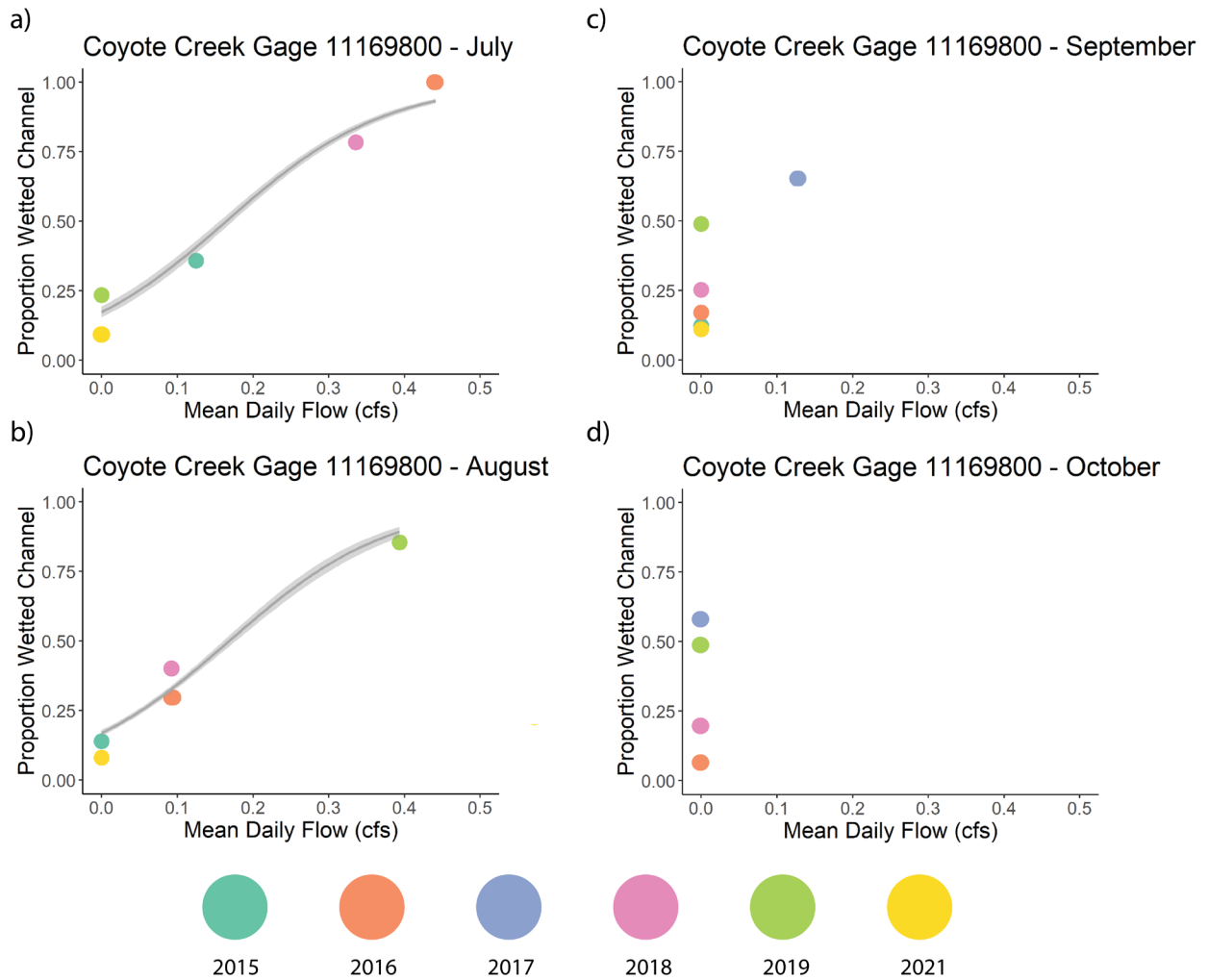
Figure S1. Relationship between the proportion of channel that remained wetted during surveys and the mean daily flow (cfs) at the time of sampling in a) July; b) August; c) September; d) October. Panels a) and b) contain a logistic regression curve.

Table S3. Summary of physical and land cover metrics for each gauge location

| Site	gauge Name	Local Slope	Mean Channel Slope	Local Landcover	Prop. Watershed Wetland	Prop. Watershed Shrub/ grassland	Prop. Watershed Developed	Prop. Watershed Forested	Prop. Watershed Agriculture
Dutch Bill Creek	40068 River Kilometer 0.68	1.23	4.44	Developed	0.28	9.42	5.84	84.45	0.01
	40387 River Kilometer 3.87	1.04	3.74	Forested	0.00	11.61	6.34	82.04	0.01
	40651 River Kilometer 6.51	1.77	7.33	Developed	0.00	15.60	8.46	75.93	0.01
Mill Creek	160201 River Kilometer 2.01	1.22	2.16	Shrub/ Grassland	0.00	6.85	4.46	85.99	2.70
	160311 River Kilometer 3.11	2.68	6.71	Forested	0.00	5.93	4.11	88.57	1.39
	160610 River Kilometer 6.10	6.20	9.08	Forested	0.00	3.86	3.79	92.35	0.00
Coyote Creek	USGS# 11169800	5.13	5.33	Forested	0.49	49.08	0.01	50.26	0.16
Aravaipa Creek	USGS# 9473000 River Kilometer 9.50	1.08	6.31	Shrub/ Grassland	0.40	85.94	0.02	13.59	0.05
Babocomari River	USGS# 9471400 River Kilometer 5.50	1.46	0.94	Shrub/ Grassland	0.32	75.45	5.26	18.96	0.01
San Pedro River	USGS# 9471550 River Kilometer 154	0.92	1.22	Shrub/ Grassland	0.30	84.19	5.27	9.73	0.51
	USGS# 9470500 River Kilometer 200	0.72	1.52	Forested	0.00	78.19	2.01	19.24	0.56
	USGS# 9471000 River Kilometer 170	1.57	0.64	Shrub/ Grassland	0.12	84.31	5.29	9.77	0.51
Rio Grande	USGS# 8358400 River Kilometer 110	0.13	0.76	Wetland	0.71	74.90	3.16	20.34	0.89
	USGS# 8355490 River Kilometer 141	0.31	0.92	Wetland	0.63	74.46	3.19	20.90	0.82
	USGS# 8354900 River Kilometer 184	0.62	1.46	Wetland	0.85	75.31	3.09	19.85	0.90
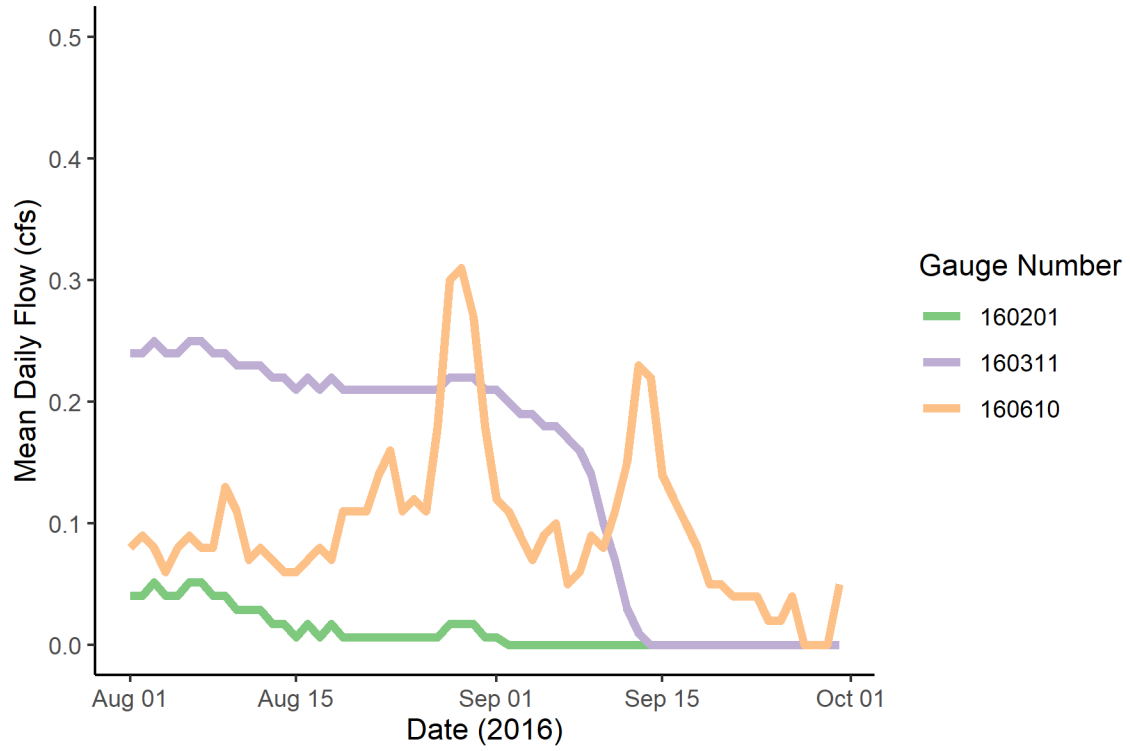
Figure S2. Streamflow at three nested gauges along Mill Creek, CA over the summer dry down in 2016. Gauge #160201, #160311, and #160610 have increasing proportion of natural land cover (wetland, forested, shrubland combined) in the upstream watershed, in that order

CHAPTER 2 | on the controls and sensitivity of intermittent stream drying

Hana Moidu, Mariska Obedzinski, Stephanie M. Carlson, Theodore E. Grantham

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Abstract

Intermittent streams comprise much of the global river network, and are expected to become more prevalent with climate change. Characterizing the expansion and contraction of intermittency in stream networks, and understanding how sensitive these dynamics are to climatic variability, is critical for predicting the trajectory of hydrologic regimes in a changing climate. Here, we consider the spatial patterns of stream intermittency, focusing on wetted channel conditions at the end of the dry season, and identify land cover, physiographic, and climate variables that influence surface water presence and variability across years. We trained statistical models with wetted channel mapping data from 25 streams over 7 years to predict both the spatial and interannual variability of the wetted channel network. We then used the models to assess intermittent stream dynamics across the Russian River watershed in northern California, USA. We found that an average of 3.7% of the stream network was reliably dry, while 16.1% was reliably wet at the end of the dry season, with the remainder of the network exhibiting variability in wetted conditions in response to antecedent precipitation. Both climatic and landscape characteristics controlled the extent of the wetted network, particularly antecedent precipitation at seasonal and annual time scales, highlighting the role of hydrologic memory in this system. Given predictions of increased climate volatility, an improved understanding of the spatial patterns and stability of dry season conditions in intermittent streams can inform climate risk assessments and strategies for protecting biodiversity and the ecosystem services that intermittent streams support.

Introduction

Intermittent streams are common throughout the world, and are characterized as having variable cycles of wetting and flow cessation (Busch et al., 2020). Though intermittency is a natural phenomenon, projected changes in temperature and precipitation patterns are expected to prolong the dry season and increase the frequency of multi-year droughts in many parts of the world (Dai, 2011). This, in turn, is predicted to intensify the low-flow period and exacerbate the duration and severity of intermittent conditions (Grimm & Fisher, 1992; Larned et al., 2010). Changes to streamflow patterns can profoundly influence ecological functioning of streams by disrupting evolutionary cues (Heim et al., 2016), altering nutrient cycles (von Schiller et al., 2011), and increasing the risk of invasion by nonnative species (Larson et al., 2009). Many endemic and imperiled species that are adapted to natural intermittency may be placed at risk of extirpation from these shifts (Jaeger et al., 2014). Furthermore, changes to hydrological regimes may reduce the ecosystem services provided by intermittent streams, such as drinking water resources (Marshall et al., 2018) and nutrient cycling (Datry et al., 2018b), which may exacerbate stressors faced by human populations (Datry et al., 2018a). Understanding the drivers of intermittent stream dynamics, as well as their sensitivity to climate variability, is critical for predicting how functioning of these systems may change under a volatile climate future.

Previous studies on temperate and arid intermittent stream dynamics have shown that as the dry season progresses, the wetted channel contracts from the full extent of the geomorphic channel network in response to declining stream discharge (Godsey & Kirchner, 2014). The spatial and temporal patterns of intermittency are affected by meteorologic, geologic, and land cover conditions (Costigan et al., 2016), with topographic relief and lithology playing a particularly important role in influencing the spatial patterns of wetted channel contraction in intermittent stream networks (Jensen et al., 2017; Lovill et al., 2018; Prancevic & Kirchner, 2019). Growing insight into the mechanisms that control wetted channel dynamics has led to attempts to model and predict intermittent stream expansion and contraction (Pate et al., 2020; Ward et al., 2018; Yu et al., 2018). These studies have explored both seasonal or subseasonal expansion and contraction of the channel network, showing that both climatic and geologic setting can predict the wetted portion of networks. These efforts have ranged in spatial scale, from small headwater catchment studies (Ward et al., 2018) to large regional analyses (Yu et al., 2018), but have rarely considered the interannual variability in patterns of intermittency.

The extent of stream drying can vary greatly depending on antecedent precipitation conditions, which are expected to be more variable with climate change (Pendergrass et al., 2017). There is evidence that intermittent streams are especially sensitive to climate fluctuations and, compared to perennial streams, are predicted to be the most at risk of hydrologic regime shifts (Dhungel et al., 2016). Yet, relatively little attention has been given to documenting and evaluating the factors that influence interannual variability in intermittent stream drying. The consideration of interannual hydrological variation in intermittent streams has largely been devoted to characterizing its effect on ecosystem processes such as nutrient cycling (Bernal et al., 2004), fish behavior (Hwan & Carson, 2016), and food chain length (Sabo et al., 2010). The few studies that have captured the interannual variability in hydrologic condition (Allen et al., 2019; Datry et al.,

2016; Hammond et al., 2021; Lapides et al., 2021; Lovill et al., 2018) highlight the dynamism of wetted extents, but none have included a spatially explicit understanding of how river networks may respond to climate variability and change. With increasing precipitation volatility and rising temperatures (Swain et al. 2018), there is an urgent need to characterize where and when intermittent streams will be buffered from, or vulnerable to, climate change.

The overall goal of this study is to characterize intermittent stream drying patterns and their stability in relation to climate variability and physical setting. We mapped dry season wetted channel extent between 2012 and 2019 at 25 streams in the Russian River watershed in northern California, USA. We used these data to develop a statistical model for wetted channel condition at the end of the dry season to evaluate the influence of a suite of land cover, physiographic, and climate variables (hereafter, the end-of-season model). Using a similar approach, we developed a model to identify factors that influence interannual variation in end-of-season wetted conditions (hereafter, the interannual variability model). Finally, the end-of-season and interannual variability models were applied across the watershed to predict extent and stability of wetted channel condition throughout the entire network.

Study Site

The Russian River watershed (3850 km²; Figure 1) encompasses parts of both Mendocino and Sonoma counties in northern California, USA. The mainstem flows 175 km from north to south and drains into the Pacific Ocean (Opperman et al., 2005). The basin is mostly underlain by Franciscan Complex, a Jurassic-Cretaceous age terrane (Berkland et al., 1972). There are also large swaths covered by hillslope deposits or alluvium. The region has a legacy of timber harvesting, which peaked in the 1950s and subsequently declined due a depletion of resources (Osward, 1972). Currently, the predominant land-use change stems from the conversion of many valleys and hillslopes in the basin to vineyards and residential development (Merenlender, 2000).

The region has a Mediterranean climate, with a highly seasonal precipitation regime. Much of the rainfall occurs from November-March, with the remainder of the year being fairly hot and dry (Gasith & Resh, 1999). Relatively few storms account for the total annual precipitation, which is highly variable year-to-year, ranging from 690-2160mm (Opperman et al., 2005). Streamflow reflects this seasonal and interannual variability in rainfall (Sumargo et al., 2020), with discharge peaking in the winter wet season and then receding through the summer dry season, and varying between years relative to antecedent precipitation. Most of the tributaries of the Russian River cease to flow in the dry season, contracting into reaches that contain a series of disconnected pools or are completely dry (Deitch et al., 2009). While recession in many watersheds begins in the low-order headwaters (Biswal & Marani, 2010), drying in the tributaries of this system tends to begin in the lower alluvial reaches and proceeds upstream, with headwater reaches often remaining wetted through inputs from groundwater and springs (Grantham, 2013), as has been reported in other arid landscapes (Stanley et al., 1997). Despite the harsh environmental conditions of these intermittent streams, remnant pools within these tributaries are important habitats for native aquatic species, including endangered Coho salmon (*Oncorhynchus kisutch*), and threatened Steelhead trout (*O. mykiss*) (Grantham et al. 2012; Obedzinski et al., 2018; Vander Vorste et al. 2020).
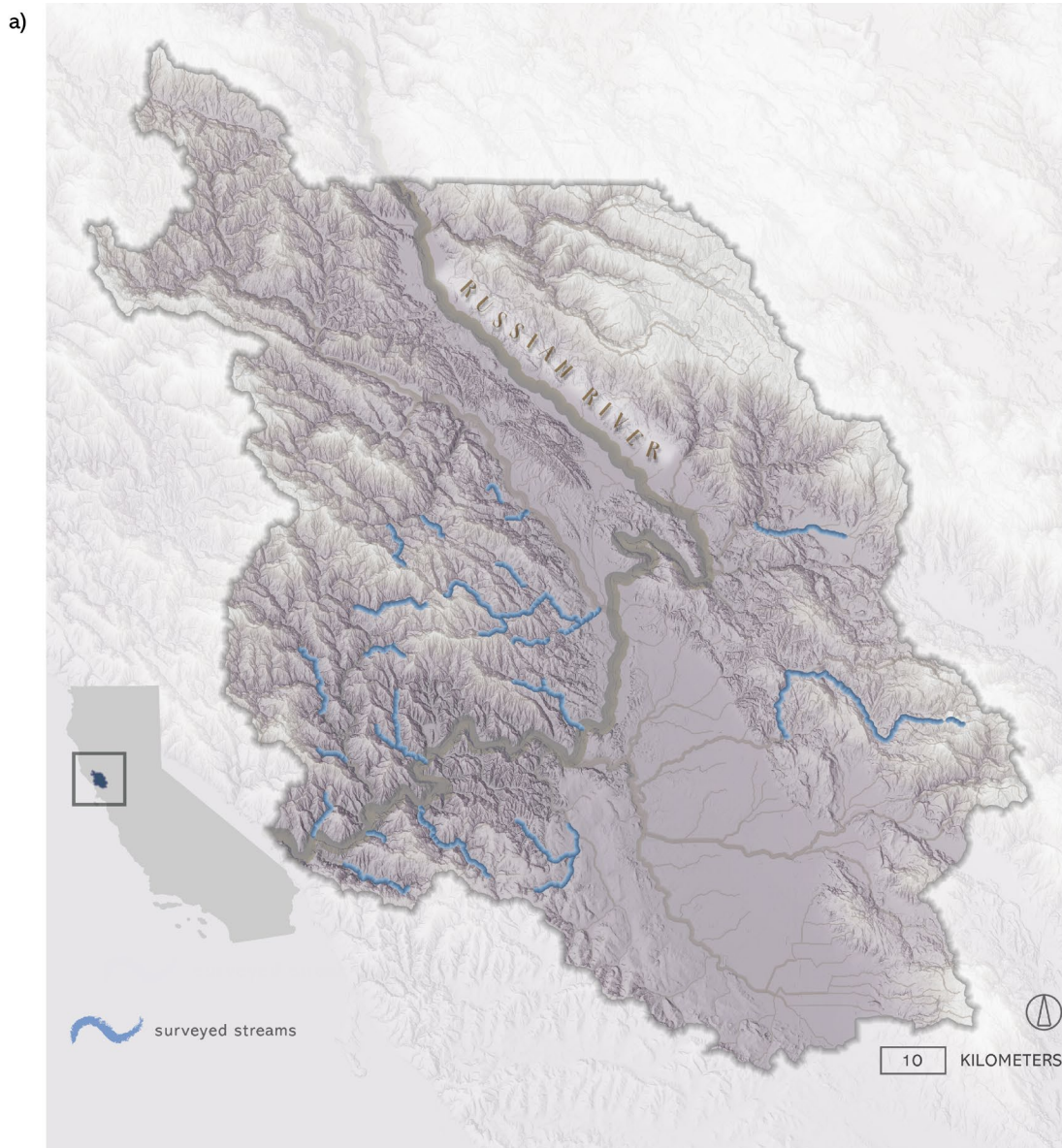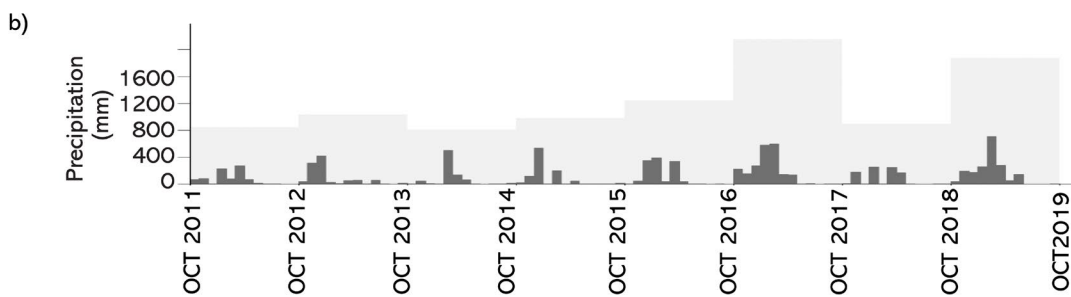
Figure 1. a) Map of the Russian River watershed in northern California, USA with the spatial distribution of the streams included in the study; b) water year precipitation (gray) and monthly (black) precipitation

Methods

Wetted Channel Mapping

Surveys of wetted channel conditions were conducted between 2012 and 2019 in 25 stream reaches (Table S1), ranging in length 0.46 km to 22.04 km, for an average total surveyed length of 84.89 km each year. Most streams were surveyed at the end of the dry season (September - October), when the extent of stream drying is greatest, while a few focal streams (Figure 2b) were surveyed biweekly to capture the change in condition during the summer dry-down period (May-October). For many streams, surveys were completed in one day, but surveys for longer streams were surveyed on consecutive days. Study streams were selected for their potential to support endangered salmon, and represent the broad range of land cover, physiographic, and climate conditions found in the Russian River watershed. For some streams, the extent of the channel that was surveyed depended on landowner access, which was subject to change yearly. The timespan within which surveys were conducted encompassed extreme low and high precipitation years (Figure 1).

To document wetted channel condition, field crews walked the length of the geomorphic channel of each stream, using a Bad Elf GPS (+/- 1 m accuracy) connected to ArcCollector on a digital tablet to map the presence of surface water. A "wet" classification was defined as visible surface water presence. Following data collection, the survey data was aggregated and delineated into 100m long reaches. The proportion of the reach length that was classified as dry along the 100m reach was calculated for each year. Interannual variability was calculated as the coefficient of variation of the end-of-season wetted reach proportion across years. Not all streams or reaches were surveyed each year and only streams with at least three years of mapping were included in this analysis (Table S1).

Model Development

The wetted channel observations were combined with a suite of geospatial variables to train models for end-of-season condition and interannual variability. Predictor variables were compiled for each 100-m reach of all study streams using land cover, physiographic, and climate characteristics that have been previously reported to influence stream expansion and contraction (Costigan et al., 2016; Prancevic & Kirchner, 2019). Climatic variables were obtained for each reach from the PRISM dataset (Daly et al., 2008) and included mean annual temperature, total annual precipitation, and total seasonal precipitation, which was calculated from monthly averages for winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November). We also calculated precipitation totals from the antecedent year, antecedent 3 years, and antecedent 5 years to explore legacy effects of precipitation. Physiographic variables included upstream area, slope, elevation, planform curvature, and surficial properties. The drainage density scaling exponent (Prancevic & Kirchner, 2019), quantifying how drainage area increases nonlinearly with downstream distance, was calculated for each subwatershed. The dominant geologic unit class, obtained from the State Geologic Map Compilation (Horton, 2017), and soil properties such as texture and runoff potential, obtained from the Gridded Soil Survey Geographic Database (Soil Survey Staff, 2016),

were calculated at the local (from a 10m buffer along each 100-m reach) and watershed scale (contributing area to each reach). Finally, percent land use/land cover obtained from the National Land Cover Database (Homer et al., 2012) and canopy density from the Sonoma County Vegetation Mapping and LiDAR Program (Dubayah & Hurtt, 2014) were calculated at the local- and watershed-scale. An extended description of the variables included can be found in the Supplementary Materials (Table S2). We calculated a correlation matrix and removed variables that were highly correlated (Pearson correlation coefficient ≥ 0.80) (Figure S1). The variables that were highly correlated were annual precipitation with winter, spring, and fall precipitation; spring precipitation with fall precipitation; antecedent 3 years' precipitation with antecedent 5 years' precipitation; medial soil with agriculture; and loam soil with high soil runoff potential and skeletal soil. For each group of highly correlated variables, we identified and removed the one that was more correlated with other variables. This process removed the annual precipitation, spring precipitation, antecedent 3 years' precipitation, medial soil, and loam soil variables from model development.

The predictor variables were combined with the wetted channel survey observations in two statistical models using the random forest method (Cutler et al. 2007; Prasad et al. 2006): one to predict the end-of-season condition and one to predict the interannual variability. For the end-of-season (EOS) model, the wetted channel was quantified as the proportion of each reach that was dry, ranging from 0-100%. For the interannual variability (IAV) model, the coefficient of variation of the end-of-season condition across the years surveyed (2012-2019) was calculated for each reach.

Model Evaluation and Application

The random forest models were implemented using the caret 6.0-86 package in R 3.4.2 (Kuhn, 2011). Random forests are a robust decision tree model, where predictions from hundreds of individual decision trees are aggregated to compute a mean predicted value. Partitioning the dataset into independent decision trees reduces variance and limits the risk of overfitting (Liaw & Wiener, 2002). A leave-one-out cross-validation method was used to assess model performance, in which models were iteratively trained with subsets of the data that randomly excluded 5 streams. The omitted sites were then returned to the training class for the next iteration, with a different subset of streams being reserved as the validation class. In each iteration, model predictions were made for the streams that were excluded from the dataset and performance was assessed by comparing observed and predicted values using R^2 and mean square error (MSE). A range of tuning parameters were tested to find optimal values for the model (Table S3). We found a marginal increase in model performance with an increase in number of trees or tree depth, with 100 trees and tuning length of 5 resulting in a model with both high performance and lower processing time. Variable selection was done by using a recursive feature elimination method (Gregorutti et al., 2017) to identify a subset of variables to train a model with comparable accuracy as when all variables are included. The importance of each predictor variable was determined using increase in MSE in predictions when a variable is permuted and node purity, which is a measure of the variance of the predictions when a given variable is a node of a decision tree. For example, if reach observations are consistently wet when "clay soil" is a node, then the

"clay soil" variable would have a high purity value. If observations have a large variance in their predicted outcome when "clay soil" is a node, then the variable would have a lower purity value. Individual conditional expectation (ICE) plots, which isolate the effect of a variable on the predicted outcome, were used to determine the direction of each variable's influence on wetted condition or variability.

The trained models were then used to predict EOS wetted conditions and interannual variability in all streams in the lower Russian River watershed (Figure 1). The upper section of the Russian River watershed was not included due to lack of LiDAR data used for topography and canopy variables. We calculated the same predictor variables used in the model for all 100-m stream reaches in the NHD dataset. Meteorologic variables were calculated from a 10-year climate record from 2009-2019 (PRISM). Since model predictions cannot be reliably made outside of the domain of the training dataset, we removed the stream reaches for which the predictor variable value fell outside the maximum and minimum bounds of the training data domain. This excluded 1.5% of the stream network, located in the lower Russian River watershed. We determined stability of intermittent stream drying patterns by relating the EOS wetted channel predictions with the IAV model predictions for each reach. "Reliably dry" reaches were defined as those with a low proportion of wetted extent (<20% of the reach) and low interannual variability (CV < 20%), while "reliably wet" reaches were defined as those with a high proportion of wetted extent (>80% of the reach) and low interannual variability (CV < 20%).

Results

Wetted channel mapping patterns

While nearly all streams in the watershed are intermittent, the extent and interannual variation of end-of-season wetted habitat varies among streams, with some streams exhibiting consistent end-of-season conditions, regardless of antecedent precipitation, while others differ greatly across years (Figure 2a). Two representative streams, Dutch Bill Creek and Mill Creek (Figure 1), show similar temporal patterns of wetted channel contraction over the summer months of 2018 (Figure 2b), with the lower reaches of both creeks becoming dry around August, but to a greater spatial extent in Dutch Bill. The creeks also exhibit distinct interannual variation in end-of-season wetted conditions (Figure 2c), with Dutch Bill Creek showing consistent drying patterns in the lower reaches between 2012-2019, while Mill Creek varies more in the lower reaches across years. Given that both watersheds share the same climate regime, this suggests that differences in hillslope routing and subsurface properties may cause this difference in wetted channel conditions between years. This pattern is consistent across the Russian River watershed; where each stream varies such that there is no unifying signal of channel contraction.
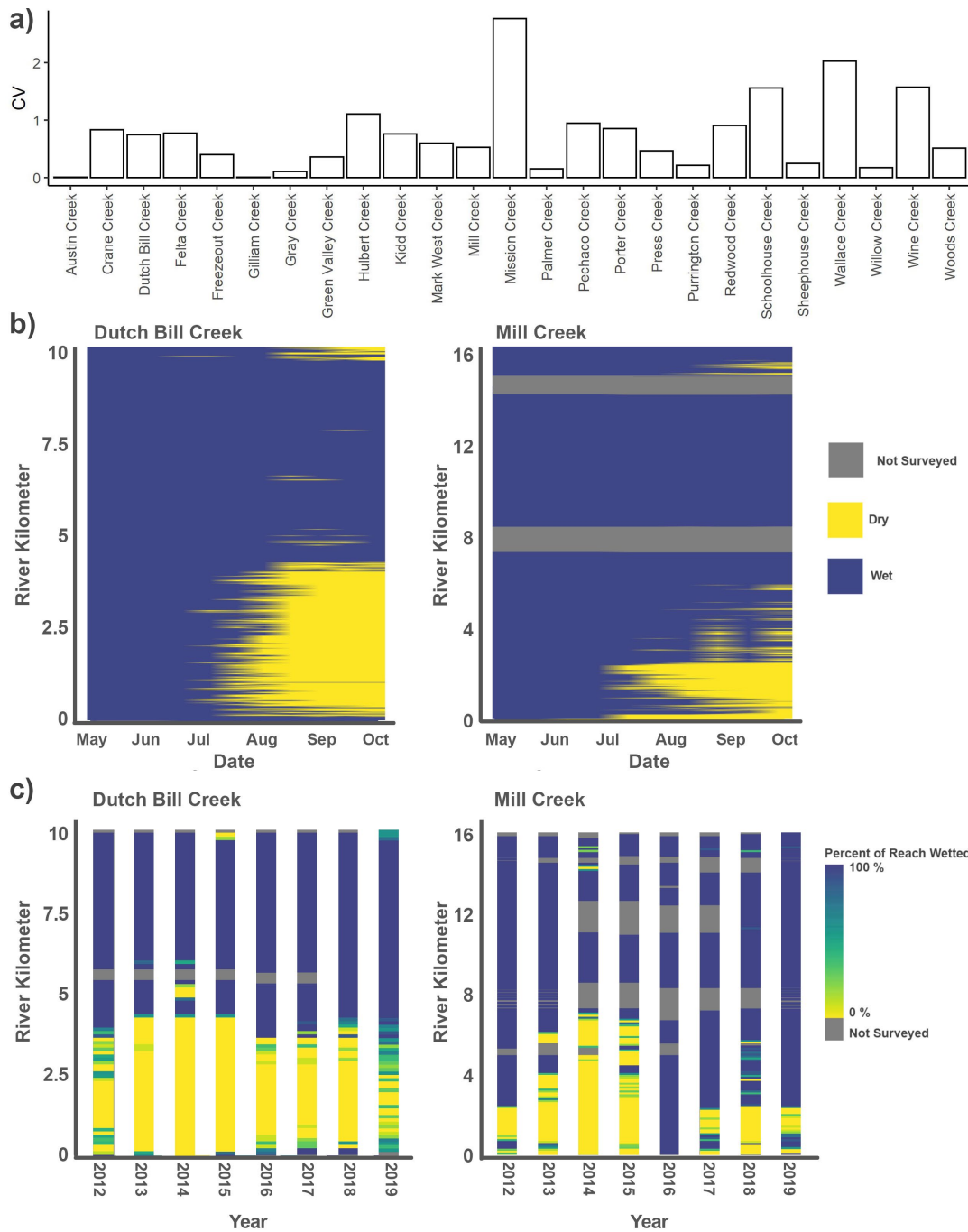
Figure 2. Variability of end-of-season condition within the watershed. Panel (a) shows overall variability in end-of-season condition for each stream surveyed, calculated by taking the coefficient of variation. Panel (b) shows the change in condition over the summer dry-down period (May-October) for two representative streams, Dutch Bill Creek and Mill Creek in 2018. Panel (c) shows the end-of-season condition in September from 2012-2019 for the same streams. For both (b) and (c), the vertical axis is river kilometer in upstream order, with 0 denoting the most downstream point. Gray denotes regions that were not surveyed due to inaccessibility.

End-of-Season predictive model

The EOS model accurately predicted the spatial extent of wetted channel conditions, with the best performing model having an R^2 of 76.7% (Figure 3a). A recursive feature elimination analysis determined 15 variables (Figure 3b) that improved model accuracy, with an R^2 of 82.2%. When comparing the predicted wetted channel extent to the observed channel extent in streams excluded from model training, we found that 77% of the predictions were within 20% of the observed condition. The EOS model was trained using data from a range of water years, including extreme wet and extreme dry years, which allowed us to understand how the watershed responds to anomalous conditions. In the wettest year surveyed (2019), 65% of the study reaches were predicted to be wet (>80% of the reach wetted at the end of the season), while 13% of the reaches were predicted to be dry (<20% of the reach wetted at the end of the season) at the end of the season. In contrast, in the driest year surveyed (2013), 51% of the study reaches were predicted to be wet compared to 18% of the reaches predicted to being dry. On average, 58% of the reaches were predicted to be wet, while 18% were predicted to be dry at the end of the season.
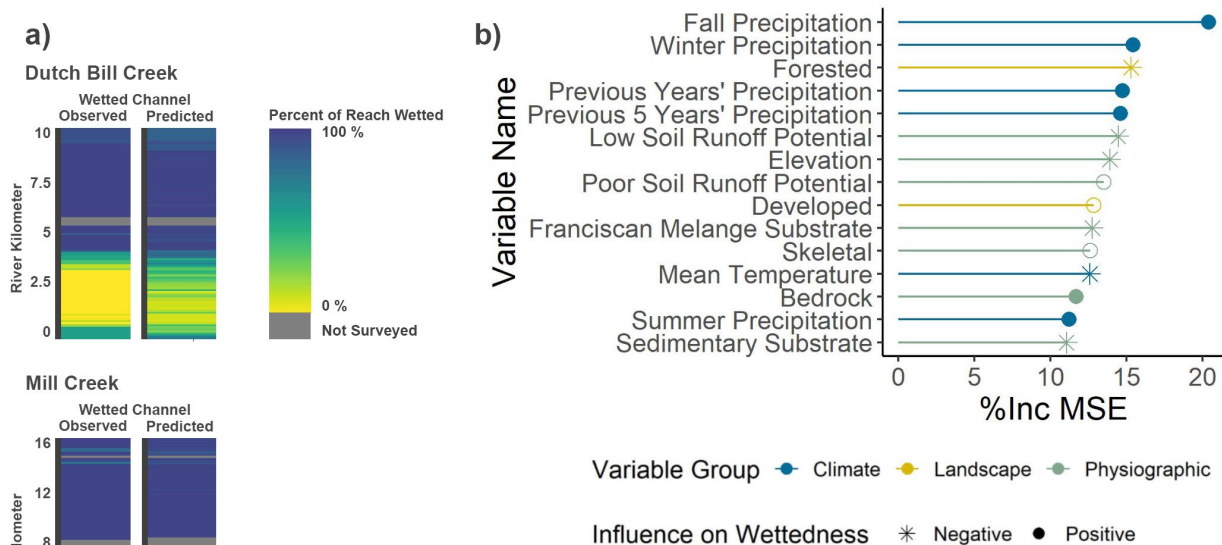

Figure 3. Performance of the end-of-season (EOS) predictive model. (a) Comparison of observed and predicted wetted channel for Dutch Bill Creek and Mill Creek, displaying EOS condition averaged across years along the stream length. The vertical axis is river kilometer, with 0 denoting the most downstream point. (b) The 15 variables selected from the recursive feature elimination with the sign of each variable's influence on channel wettedness, determined using individual conditional expectation plots.

Climate variables were the most influential in the EOS models, as determined by rankings in both MSE and node purity (Figure S2). Long-term precipitation (LTP), including antecedent year and 5-year totals, as well as seasonal precipitation metrics, were among the top important

variables. All precipitation metrics had a positive influence on reach wettedness, while mean annual temperature had a negative influence (Figure 3c). Physical variables were also influential, particularly the soil runoff potential, as well as different land cover metrics. Partial dependence plots (Figure S3-4) illustrate the influence of physical surface and near-subsurface variables relative to LTP. They show that reaches were more likely to be wet when the LTP was higher, but that physical properties mediate the influence of LTP. For example, the positive effect of LTP on wetted conditions is dampened in watersheds predominantly underlain by metamorphic rock (Figure S3), but is amplified in those underlain by sedimentary rock (Figure S4).

Interannual variability model

The IAV model was trained on the observed interannual variance of each reach's EOS condition, along with the variables outlined in Table S2. Unlike the EOS model, the IAV model did not include time-varying climatic data, and instead included long-term variables of precipitation and temperature variance to characterize each stream reach. The best performing IAV model had an R^2 of 68.3% and highlighted differences within and among the study streams. For example, Dutch Bill Creek and Mill Creek (Figure 4a) have a very different wetted channel pattern, but the IAV model is able to capture the degree and distribution of interannual variability for both. For regions that show low interannual variability, the IAV model is able to predict both reliably wet and reliably dry sections.
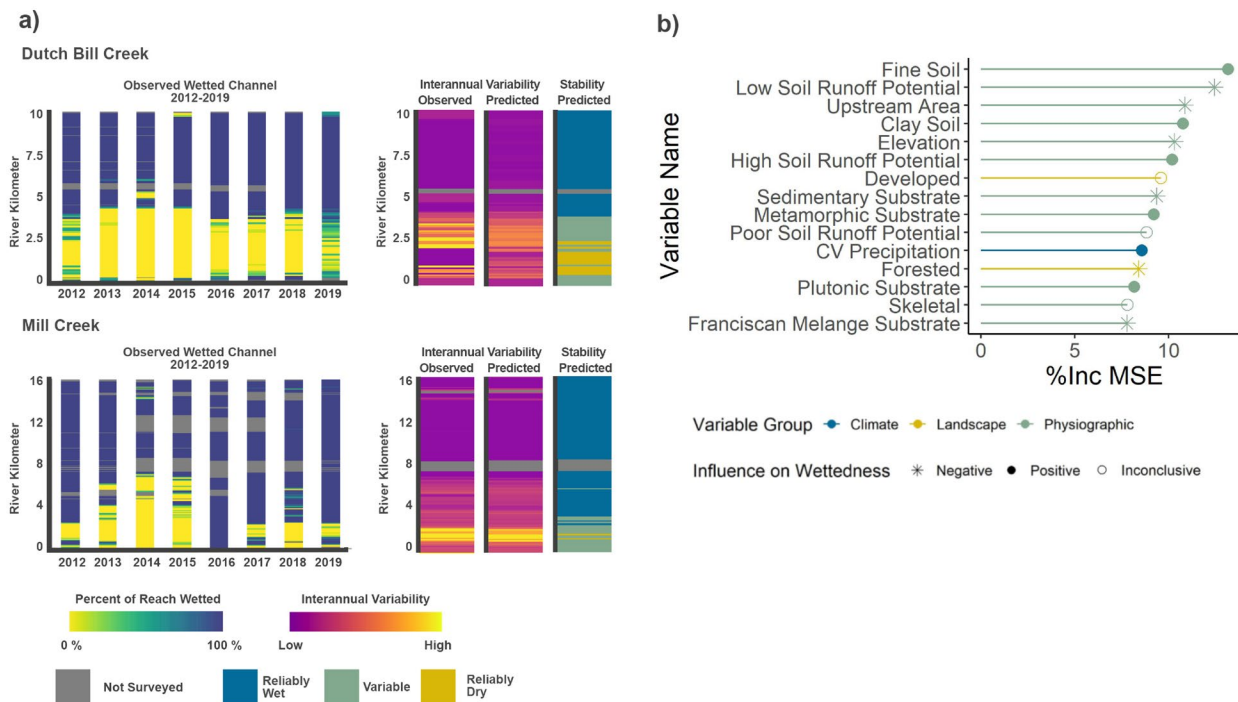

Figure 4. Performance of the interannual variability (IAV) model. (a) Comparison of observed wetted channel for Dutch Bill Creek and Mill Creek between 2012-2019 with the observed and predicted interannual variability, as well as streamflow stability, along the stream length. Streamflow stability is characterized through "reliably dry" reaches, which are defined as those

with a low proportion of wetted extent (<20% of the reach) and low interannual variability (CV < 20%), while "reliably wet" reaches are defined as those with a high proportion of wetted extent (>80% of the reach) and low interannual variability (CV < 20%). The vertical axis is river kilometer, with 0 denoting the most downstream point. (b) The 15 variables selected from the recursive feature elimination with the sign of each variable's influence on variability, determined using individual conditional expectation plots.

Important predictor variables (Figure S5) were determined using both percent increase in MSE and node purity. A recursive feature elimination analysis (Figure 4b) determined 15 variables that were sufficient in maintaining model accuracy, with an R^2 of 63.9%. These variables primarily relate to the physical surface or near-subsurface conditions, including geologic classes, soil permeability, and some landcover metrics. Geologic classes, including Franciscan Melange and sedimentary substrate, as well as low soil runoff potential, upstream, area, and elevation had a negative influence on end-of-season condition variability. In contrast, fine soil, clay soil, high soil runoff potential, and metamorphic substrate had a positive influence on variability.

Stability of intermittent stream drying patterns to climate variability

Applying our models to the whole watershed provides insights into the sensitivity of the wetted stream network to climate variability. For the driest year included in this analysis (2013), 9.8% of the entire stream network in the study area was predicted to be dry (<20% of reach wetted) and 46.7% of the stream network wet (>80% of reach wetted) at the end of the season. In contrast, for the wettest year (2017), 6.5% of the stream network was dry, compared to 71.1% of the stream network being wet.

Application of the results from the EOS model and the IAV models to predict stability of streams within the lower and middle Russian River watershed indicate that 3.7% of the watershed can be classified as reliably dry, while 16.1% of the watershed is classified as reliably wet at the end of the dry season (Figure 5). The remaining reaches in the watershed are more variable in their EOS condition, either due to high variance in surface water presence, or because the response is neither strongly wet nor dry. In terms of the spatial distribution of reliably wet and reliably dry regions, 51% of the reliably dry reaches are located in the lower sections of tributary streams, within a distance of 3 kilometers from the Russian River, compared to only 10% of the reliably wet reaches.
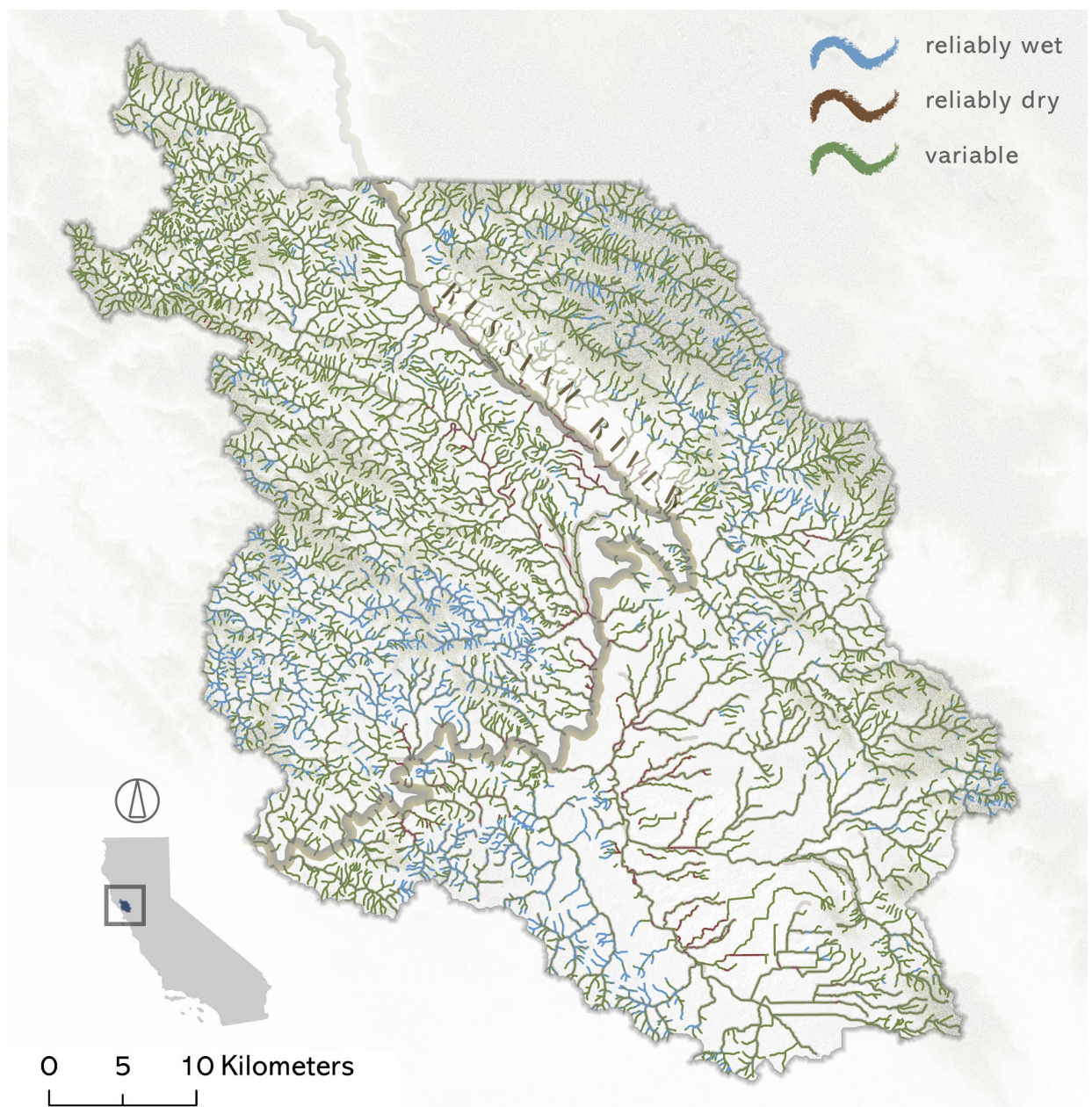
Figure 5. Stability of tributaries in the Lower and Middle Russian River watershed. "Reliably dry" reaches are defined as those with a low proportion of wetted extent (<20% of the reach) and low interannual variability (CV < 20%), while "reliably wet" reaches are defined as those with a high proportion of wetted extent (>80% of the reach) and low interannual variability (CV < 20%)

Discussion

We developed two models to characterize intermittent stream drying patterns in relation to climate variability, using dry season wetted extent surveys for 25 streams in the Russian River watershed, across a range of water years. Our results show that end-of-season condition of streams vary both spatially and temporally, depending on physical setting and antecedent climatic conditions, with precipitation in prior seasons and years having a particularly influential

effect. The models we developed to predict the end-of-season condition and the interannual variability both had strong predictive accuracy, with an R^2 of 76.7% and 68.3%, respectively. The trained models were applied across all streams in the lower Russian River watershed to characterize the stability of intermittent stream drying patterns to interannual climate variability. Accordingly, we were able to characterize streams based on their sensitivity to climate and identify stream reaches predicted to be reliably dry, those responsive to antecedent precipitation, and those predicted to be reliably wet and thus buffered to climate variability.

Controls on end-of-season channel dynamics

Results from the EOS model suggest that climatic variables have a dominant influence on wetted channel conditions. In addition to wet season precipitation, cumulative precipitation from the previous year and previous 5 years all had a significant influence on EOS wetted conditions. This points to the importance of hydrologic memory, and the legacy effects of antecedent precipitation in controlling wetted channel conditions. Hydrologic memory has been described as the phenomenon of the landscape retaining the effects of a hydroclimatic event long after the atmosphere does (Jacobs et al., 2020). In areas with highly variable precipitation, such as Mediterranean climates, watersheds exhibiting hydrologic memory can buffer stream hydrologic responses to climate variability. For example, an unusually dry year may not exhibit the same degree of stream drying if there was high precipitation in previous years. This has been expressed in the literature; looking at this potential influence of past precipitation, Nippgen et al. (2016) used 21 years of daily streamflow and precipitation data from five watersheds in North Carolina to show that the previous year's precipitation was as important as that year's precipitation for streamflow. We found that surface water presence is affected by precipitation record at even longer time scales, which could buffer the stream network from interannual precipitation variability.

The expression of hydrologic memory is spatially heterogeneous, and depends largely on the physical variables that affect subsurface, or near-surface, storage. Results from partial dependence plots show that physical variables like geology can either amplify or diminish antecedent precipitation effects. Areas underlain with sedimentary rock augment the influence of previous years' precipitation on end-of-season wetness, while areas underlain with metamorphic rock dampen the influence of previous years' precipitation. The importance of the underlying physical structure in water storage and streamflow response has been considered by others (Tague & Grant, 2004; Hahm et al., 2019a; Katsuyama et al., 2005), who have shown that storage capacity is largely dependent on properties like bedrock geology, soil depth, or degree of weathering. Recent work has shown that "rock moisture", water held within weathered bedrock, can hold significant proportions of annual rainfall, thus regulates the timing of streamflow (Rempe & Dietrich, 2018) and extent of the wetted channel (Lovill et al., 2018). Indeed, regions underlain by more permeable bedrock have been shown to have higher storage and baseflow (Pfister et al., 2017), as well as higher transit times and different flow paths (Tetzlaff et al., 2009). Recent modeling work on intermittent stream hydrology has also shown that soil type is a major control on the spatial distribution of flow generation, and that unsaturated storage dynamics largely mediated the thresholds and pathways of flow (Gutierrez-Jurado et al., 2019). Further, the

mechanisms that underpin the timing and extent of streamflow are in part due to the depth and permeability of the underlying soil, leading to spatiotemporally varying surface water presence during the dry season (Gutierrez-Jurado et al., 2021). This interplay between long term climate patterns and the highly localized influence of the underlying physical structure results in a heterogeneous wetted channel response, as is shown by our findings.

The importance of the critical zone moisture storage on subsurface moisture storage and surface water presence cannot be discounted, and the growing body of work on the subject (Brooks et al., 2015) has shown how these physical characteristics can decouple environmental responses from precipitation variability (Hahm et al., 2019b). This understanding translates to wetted channel dynamics, with regions underlain by deeply weathered bedrock shown to sustain surface water flow much longer than nearby regions with a shallow critical zone (Lovill et al., 2018). Similarly, results from this study show that longer term precipitation can buffer regions from anomalous climatic conditions depending on the subsurface storage characteristics.

Variability and stability of streams in a non-stationary climate

While it is important to understand factors that control the extent of the wetted channel in a given year, the factors that predict the interannual variability of stream responses provide valuable insight as well. Current climate models predict a shifting climate regime, with already variable regions expected to become even more volatile (Horne et al., 2019). For example, in California, which experiences a Mediterranean climate with strong interannual variability, future climate is projected to have an exacerbated seasonal cycle, with rapidly alternating drought and flood periods (Swain et al., 2018). This increase in anomalous and extreme events will likely intensify intermittent stream conditions, and may shift systems from perennial to intermittent (Datry et al., 2014; Doll & Schmied, 2012; Larned et al., 2010). Given that a river's flow regime acts as a first order control on its ecological and biogeochemical processes (Power et al., 1995), changes to a system's flow regime can alter its integrity and capacity to support specific biotic communities (Cid et al., 2020; Grimm et al., 2013). Understanding how the river network responds to precipitation variability can provide insight into its stability under a non-stationary climate and help predict changes in streamflow patterns.

The variability model developed in this paper can be used to characterize the river network and allows us to understand its long-term functioning. Streams within the Russian River watershed all fall within the same Northern Coast Ranges hydrogeologic province, but we see a large variation in stream drying dynamics across space and time. Our results show that in an extreme wet year, the predicted proportion of wet reaches is nearly double that in an extreme dry year, while the predicted proportion of dry reaches is half. By applying the end-of-season and interannual variability models to the whole watershed, we can identify where these wet and dry reaches persist regardless of antecedent conditions. For example, regions of high variability, which respond proportionally to antecedent conditions, are vulnerable to a volatile climate and are at risk of increasing in severity of intermittent condition and habitat fragmentation. These changes can have profound effects on ecosystem functioning and species survival, where suitable habitats may become ecological traps in highly responsive systems (Vander Vorste et al., 2020).

Though many species are adapted to intermittent conditions, increased severity of drying has been found to influence the persistence (Jaeger et al., 2014) and genetic composition of populations (Golden et al., 2021). In all likelihood, projected climate change will alter conditions faster than some species can respond (Lytle & Poff, 2004; Morrongiello et al., 2011). In contrast, regions of low variability, which are stable in their EOS condition regardless of the antecedent conditions, are buffered from anomalous climate events. From an ecological perspective, we can use this understanding to identify wet reaches with low variability as candidates for climate refuges, with reliable habitat year to year.

Implications for management

Understanding where viable habitat exists within a stream network is a key management challenge, but existing strategies are often based on static conditions. Tonkin et al. (2019) recently called for novel strategies to adaptively manage river ecosystems, with a focus on models that incorporate increasing climatic variability. We address this directly by developing models that build in the nonstationarity of climate projections. The tools developed from these models can be applied to identify reaches of relative stability and concern, as well as determine areas that are vulnerable to increased intermittency. The ability to predict where the wetted channel will persist through the dry season is critically important for sustaining aquatic biodiversity in arid and semi-arid regions, and can be used to target conservation and restoration decisions. Conversely, regions that are vulnerable to increased intermittency can be targeted for further monitoring and habitat recovery strategies. That said, a distinction must be made that the models and results presented here are with respect to the end-of-season condition. Regions identified as "reliably dry" may not provide suitable habitat for aquatic organisms at the end of the summer, but may be important habitat during earlier phases of species' life cycle, such as spawning or rearing (Erman & Hawthorne, 1976; Hooley-Underwood et al., 2019; Meyer et al., 2007).

Limitations and further research

The results from this study show that empirical observations of wetted channel conditions coupled with readily available climatic and physical features of the stream network can provide valuable insights into the temporal and spatial dynamics of intermittent stream drying. However, limitations in the availability, resolution, and accuracy of geospatial variables constrained our ability to represent all the physical factors likely to influence wetted conditions. For example, geological variables were only available as coarse resolution classes, which only represented surficial components and not the subsurface structure. Previous studies have shown that subsurface geology (Day, 1980), depth to bedrock (Svec et al., 2005), and thickness of alluvium (Lovill et al., 2018) all affect the distribution of wetted channels but could not be incorporated into our analysis. Another limitation of our approach is the difficulty in distinguishing controls on stream drying from anthropogenic influences. Many of the reaches surveyed to calibrate the models presented here reflect a legacy of land use change in the watershed, which includes a history of intensive logging, agriculture, and water withdrawals. While we included some variables in the models to account for land use change, there were no data available to represent water-use pressures and alteration in stream channel morphology, which could significantly

influence stream drying patterns. Nevertheless, the omission of these factors did not appear to substantially affect the models, given their high overall predictive performance.

Given that our models were calibrated to a single watershed in a coastal Mediterranean climate system, the utility of the approach in modeling wetted conditions in other intermittent stream contexts requires further exploration. Because performing field-based wetted channel surveys over multiple years require significant time and resources, wetted condition information obtained from remotely sensed observations may offer a alternative, cost-effective, means of building a model training dataset. Future studies using remote sensors should be able to replicate the wetted channel condition data used in this study, at least in stream systems with limited canopy cover and high visibility of the stream channel. This analytical framework could also be adapted for predicting other relevant hydrological metrics, including timing of disconnection or rewetting, which would advance our understanding of how intermittent stream ecosystems may respond to climate change.

Further research is needed to expand on these findings and clarify the mechanistic connections between climate and physical variables. We found that precipitation at multiple timescales was important in predicting channel wetness, but it is unclear how these different precipitation metrics then translate to surface water presence. Of the few studies that have considered the response of precipitation at multiple timescales, Spencer et al. (2019) found that the discharge response to multi-year precipitation was controlled by bedrock storage, which regulated the baseflow, whereas event-scale rainfall response was controlled by soil and glacial till storage. However, this work was characterizing perennial streams, and more work is needed for intermittent streams in regions with seasonal precipitation. Future research focusing on the mechanisms by which both multi-year and event-scale precipitation translate to wetted channel dynamics and how the underlying physical properties that facilitate both short- and long-term water storage would greatly shape our understanding of these dynamic systems.

Conclusion

Understanding the spatial and temporal distribution of stream intermittency and variability is of fundamental importance for hydrology and freshwater ecology, with implications for sustaining imperiled and endemic species. By combining field observations of wetted channel extent with land cover, physiographic, and climate variables, we developed two models to predict both the extent and variability of the wetted network. We expanded this model to the entire watershed to further understand network dynamics and explore the stability of end-of-season conditions to climate variability. Climatic variables largely controlled the extent of the wetted network at the end of the season, with an emphasis on long-term precipitation, pointing to the importance of hydrologic memory. The degree to which hydrologic memory contributed to the condition of a reach was dependent on the underlying physical structure. Regions underlain by sedimentary rock tend to amplify hydrologic memory, while regions underlain by metamorphic rock tend to diminish hydrologic memory. These surficial characteristics also strongly influenced the variability of the wetted network. Given that climate predictions are calling for increased precipitation volatility, understanding the spatiotemporal drying dynamics of intermittent

streams can inform climate risk assessments and strategies for protecting biodiversity and the ecosystem services that intermittent streams support.

Acknowledgements

Supplementary Information

	2012	2013	2014	2015	2016	2017	2018	2019	Average
Austin Creek					5.62	6.18	6.11	6.23	**6.03**
Crane Creek		1.64				1.92	1.93	1.93	**1.85**
Dutch Bill Creek	6.78	6.76	6.78	9.27	9.2	9.25	9.63	9.72	**8.42**
Felta Creek	1.68	3.07	3.06	4.25	4.28	3.64	3.64	4.33	**3.49**
Freezeout Creek				1.48	1.46	1.37	1.51	1.52	**1.46**
Gilliam Creek				2.56	2.61	2.74	2.56	2.75	**2.64**
Gray Creek				6.32		4.19	6.26	6.32	**5.77**
Green Valley Creek	5.55	6.57	6.55	3.44	5.41	5.4	5.41	8.52	**5.86**
Hulbert Creek				2.25	1.49	7.84	7.96	7.96	**5.50**
Kidd Creek				2.45	2.35	2.1	2.45	2.45	**2.36**
Mark West Creek	4.15	3.94	13.56	4.49	19.09	6.92	22.04	22.17	**12.04**
Mill Creek	11.9	11.54	9.27	9.51	11.84	12.7	14.42	16.59	**12.22**
Mission Creek				0.58		0.58	0.58	0.58	**0.58**
Palmer Creek			2.62	2.61	3.08	2.94	2.91	3.08	**2.87**
Pechaco Creek				1.89		2.48	2.29	2.48	**2.28**
Porter Creek	2.27		5.33	7.36	7.3	0.74	7.37	7.39	**5.39**
Press Creek		0.46	0.47		0.62			0.63	**0.54**
Purrington Creek	2.04	2.82	2.97	2.89	2.48	2.85	3.05	3.38	**2.81**
Redwood Creek	1.17		2.96	4.77	4.65	4.57	4.57	7.15	**4.26**
Schoolhouse Creek				1.13	0.54	0.84	1.12	1.13	**0.95**
Sheephouse Creek				3.4	3.35	3.28	3.65	3.65	**3.47**
Wallace Creek		2.35	2.33	2.79	2.65	2.3	2.49	2.81	**2.53**
Willow Creek			3.64	5.86	5.84	5.82	5.86	5.86	**5.48**
Wine Creek	0.99	1.59	1.63	1.47	1.86	1.85	1.77	1.93	**1.63**
Woods Creek			1.69	3.74	3.69	4.14	4.09	4.25	**3.6**
Total	36.53	40.74	62.86	84.51	99.41	96.64	123.67	134.81	84.89

Table S1. Yearly stream length (in kilometers) of each tributary surveyed included in this study

	Variable	Operation	Ream Metric (RM) / Upstream Area Metric (UM)	Data Source, Description, and Resolution	Variable Classes
Climatic‡	Temperature	Mean	RM	PRISM (Daly et al., 2008) distributes modeled daily temperature interpolated based on local stations *Resolution: 4 kilometers*	N/A
	Precipitation	Annual total, seasonal totals, totals from antecedent year, 3 years, and 5 years	RM	PRISM (Daly et al., 2008) distributes modeled daily precipitation interpolated based on local stations *Resolution: 4 kilometers*	N/A
Physio-graphic	Slope	Mean	RM	The mean slope of the reach, determined from a 1-meter LiDAR DEM (Dubayah & Hurtt, 2014) *Resolution: 4 kilometers*	N/A
	Elevation	Mean	RM	The mean elevation of the reach, determined from a LiDAR DEM (Dubayah & Hurtt, 2014) *Resolution: 1 meter*	N/A
	Upstream Area	Calculated using ArcGIS watershed tool	RM	The upstream contributing area from the most downstream point of the reach *Resolution: 1 meter*	N/A
	Curvature	Calculated using ArcGIS by taking the second derivative of a DEM surface	RM	The shape or curvature of the slope, determined from a LiDAR DEM (Dubayah & Hurtt, 2014) *Resolution: 1 meter*	N/A
	Drainage density scaling exponent	Calculated by determining scaling of stream length and drainage area (L~A) for a given subwatershed	UAM	Calculated using a LiDAR DEM (Dubayah & Hurtt, 2014) *Resolution: 1 meter*	N/A

Physical surface & subsurface	Geology	Percent coverage: dividing the total area of each class in the upstream watershed by the total upstream watershed area	RM & UAM	The State Geologic Map Compilation a standardized, vector-based, state geologic map database of the contiguous U.S. (Horton, 2017) *Resolution: 30 meters*	Unconsolidated or Alluvium
					Franciscan Melange
					Metamorphic
					Plutonic
					Volcanic
					Sedimentary
	Soil texture	RM: dominant class UAM: Percent coverage - dividing the total area of each class in the upstream watershed by the total upstream watershed area	RM & UAM	Gridded Soil Survey Geographic (gSSURGO) Database contains the most detailed level of soil geographic data developed by the National Cooperative Soil Survey (Soil Survey Staff, 2016) *Resolution: 30 meters*	Bedrock
					Gravel
					Skeletal
					Medial
					Loam
					Fine-Silt
					Clay
	Soil Runoff Potential	RM: dominant class UAM: Percent coverage - dividing the total area of each class in the upstream watershed by the total upstream watershed area	RM & UAM	Gridded Soil Survey Geographic (gSSURGO) Database contains the most detailed level of soil geographic data developed by the National Cooperative Soil Survey (Soil Survey	Group A: deep, well to excessively drained sands or gravels and have a high rate of water transmission
					Group B: moderately deep to deep, moderately well to well drained soils with moderately fine to moderately coarse textures

Land Cover				
			Staff, 2016) *Resolution: 30 meters*	Group C: contains a layer that impedes downward movement of water and soils with moderately fine to fine structure
				Group D: clay soils with a high swelling potential, soils with a permanent high water table, soils with a claypan or clay layer at or near the surface and shallow soils over nearly impervious material
Land Cover	Land use	RM: dominant class UAM: Percent coverage - dividing the total area of each class in the upstream watershed by the total upstream watershed area	RM & UAM	National Land Cover Database 2016 provides land use data based on Landsat imagery (Homer et al., 2012) *Resolution: 30 meters*
				Developed (low, medium, and high density)
				Barren
				Deciduous, evergreen, and mixed forest
				Agricultural land
				Wetland
	Canopy density	Mean	UAM	LiDAR-derived canopy density (Dubayah & Hurtt, 2014) *Resolution: 1 meter*
				N/A

Table S2. Variables that were included in the predictive model. The dagger symbol denotes variables that were included in the end-of-season model only; all other variables were included in both the end-of-season and interannual variability model. Some variables were computed for the reach, while others were computed as a percent coverage or mean of the upstream area.

Model Test	1	2	3	4	5	6	7	8	9	10
Number of Trees	50	50	100	100	500	500	100	100	100	100
Tuning Length	5	10	5	10	5	10	2	15	5	10
Training Control	LOO CV	LOO CV	LOO CV	LOO CV	LOO CV	LOO CV	LOO CV	LOO CV	None	None
R^2	74.31	74.80	76.75	75.93	76.61	76.46	75.47	76.29	87.08	86.96

Table S3. Model test to determine tuning parameters for optimal model performance for the end-of-season model. "Number of Trees" refers to the number of decision trees to generate. The "Tuning Length" refers to the number of drawn candidate variables at each split. The "Training Control" refers to the resampling method used; in this case, a Leave-One-Out Cross-Validation (LOOCV) was used, in which models were iteratively trained with subsets of the data that randomly excluded 5 streams.
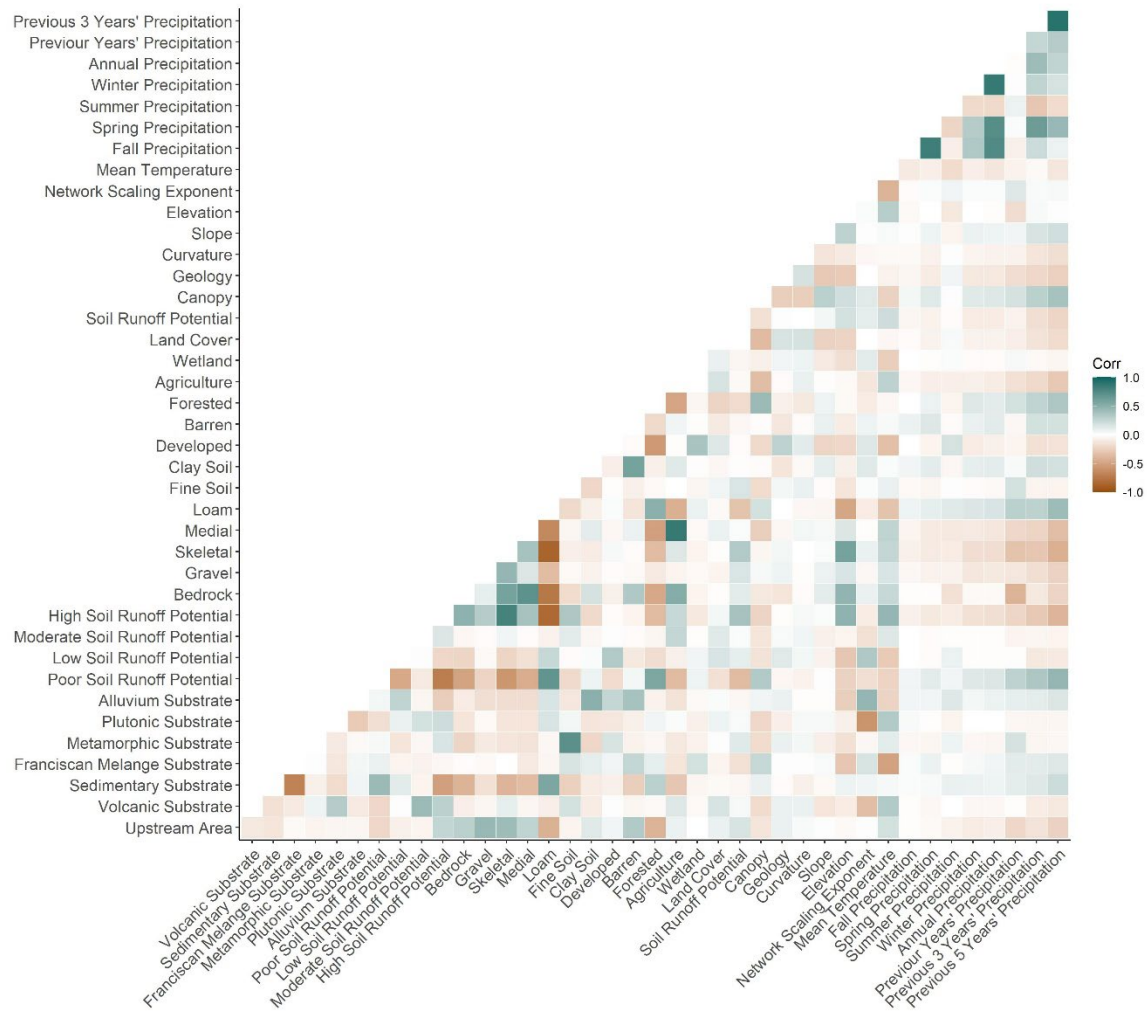
Figure S1. Correlation matrix used for variable selection for the random forest models, calculated using the Pearson Correlation Coefficient. Variables with an absolute correlation ≥ 0.8 were excluded from model development.
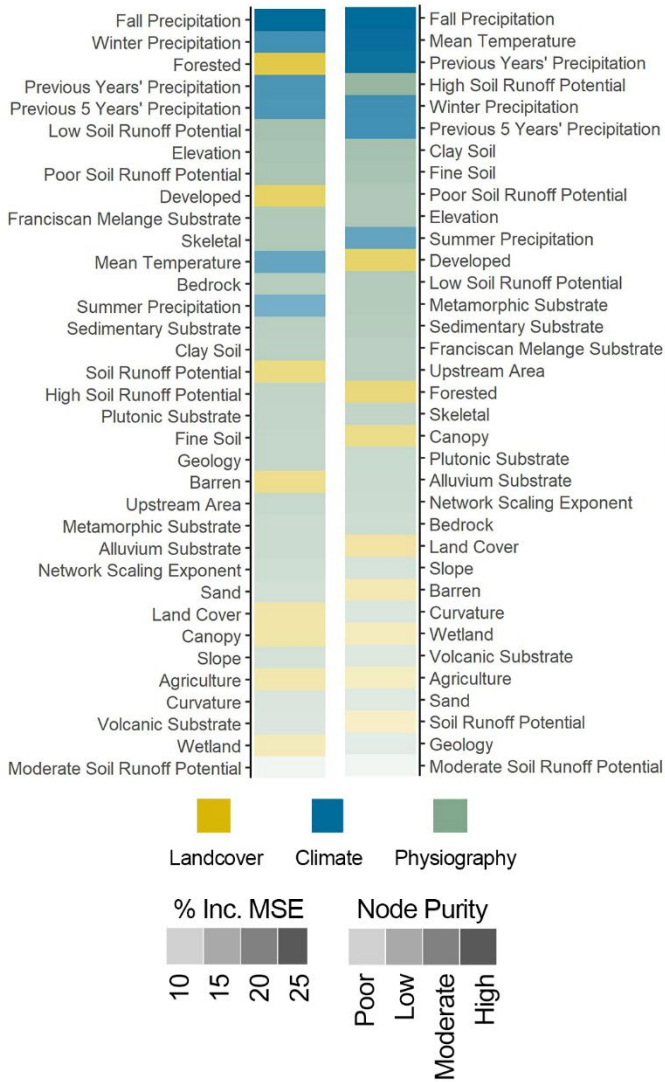
Figure S2. Variable importance for the end-of-season model determined using both the increase in MSE of predictions when a variable is permuted, as well as node purity. Node purity is a measurement of the decrease in residual sum of squares when the variable is included.
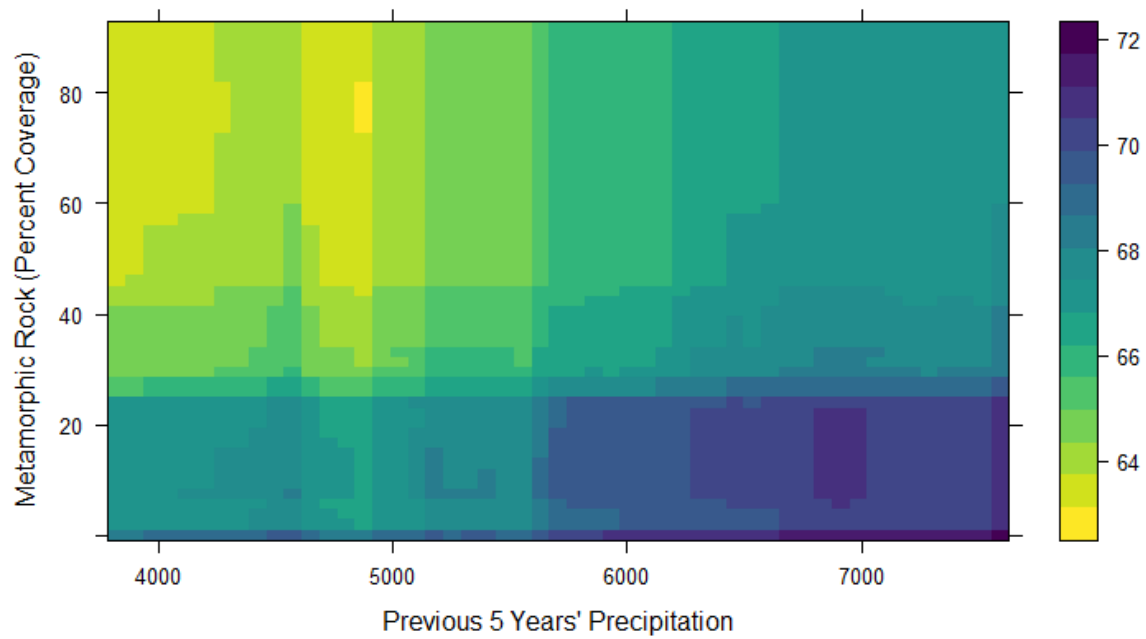
Figure S3. Partial dependence with metamorphic and previous 3 years' precipitation. Colour denotes reach wettedness, with yellow being drier and blue being wetter.
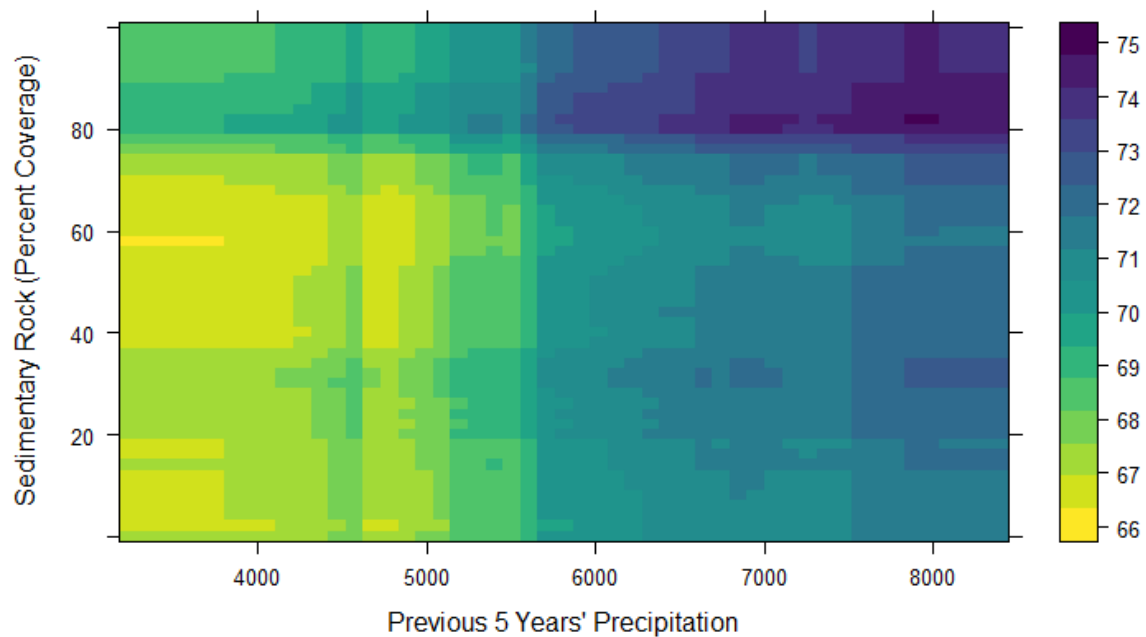
Figure S4. Partial dependence with sedimentary rock and previous 3 years' precipitation. Colour denotes reach wettedness, with yellow being drier and blue being wetter.
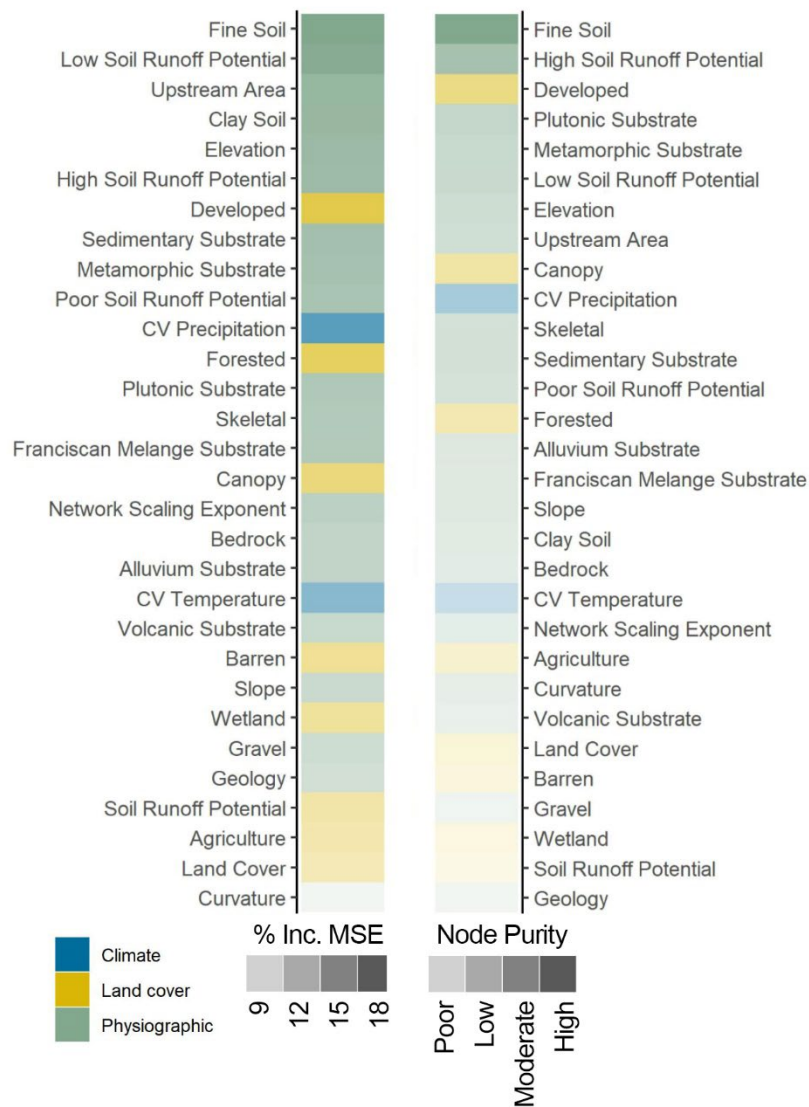
Figure S5. Variable importance for the interannual variability model, illustrating rankings based on the increase in MSE when a variable is permuted and on node purity, a measurement of the decrease in residual sum of squares when the variable is included.

CHAPTER 3 | on the ecological consequences of shifting habitat mosaics

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Abstract

Intermittent streams that cease to flow during dry periods represent more than half of the global river network, and are particularly common in arid and semi-arid regions. They are characterized by high spatial and temporal variability in aquatic habitat, forming a shifting habitat mosaic that supports diverse assemblages of native and endemic species. Climate projections for much of the world predict greater variation in precipitation and increasing drought severity, suggesting a need to better understand species' responses to habitat variability within intermittent stream ecosystems. Here we explored changes in the distribution and abundance of aquatic vertebrates in response to a wide range of annual hydrologic conditions within a Mediterranean-climate intermittent stream in California. We conducted wetted habitat and vertebrate abundance surveys during the dry season for seven years, spanning both extreme wet and extreme dry annual precipitation conditions, and characterized the variation in the size, persistence, and spatial configuration of wetted habitats in relation to the observed abundance and composition of fishes, amphibians, and aquatic reptiles. We characterized the habitat mosaic using a k-means clustering approach, and identified three habitat types with distinct size, persistence, and connectivity distributions. We found that some wetted habitat units persisted across all years, regardless of antecedent precipitation, whereas others dried in all but the wettest years. We determined that persistent pools, a subset of wetted habitats present in the stream, support diverse assemblages of native species even during extreme dry conditions, while transient pools act as important habitat for particular species and life stages, including a young-of-year minnow species. Linear mixed models indicated that species' abundances were influenced by habitat quantity, quality, and connectivity. Our results suggest that intermittent streams can be characterized as shifting habitat mosaics that support unique species and life stages across space and time and play an important role in maintaining regional aquatic biodiversity.

Introduction

Intermittent streams, characterized by a cessation of flow during dry periods (Boulton et al., 2017), are widespread across the world and make up a large proportion of the stream network in many regions (Messager et al., 2021). These systems support rich and unique biological communities (Meyer et al., 2007) with native taxa that are adapted to the temporary nature of these waterways (Stubbington et al., 2017; Kerezsy et al., 2017). Further, intermittent streams provide important ecosystem services (Koundouri et al., 2017; Pastor et al., 2022), including water provision, flood control, nutrient cycling, and support of downstream water quality and productivity (Biggs et al., 2017). Despite their ubiquity and environmental importance, intermittent streams remain vulnerable to numerous threats, including altered climate regimes (Larned et al., 2010), anthropogenic disturbance (Chiu et al., 2017), and changing regulatory protections (Keiser et al., 2022). Given these threats, an improved understanding of intermittent stream dynamics and their role in supporting ecosystem resilience is required (Lane et al. 2022).

Stream drying and contraction leads a heterogeneous riverscape, moving between flowing reaches, isolated wet patches, and dry channels that collectively form a shifting habitat mosaic. The term "shifting habitat mosaics" was introduced by Stanford et al. (2005) as a fundamental characteristic of fluvial landscapes. This concept was initially used to describe spatiotemporal changes to the patterning of available habitat in relation to flood pulses, but can also be applied to intermittent systems and stream drying dynamics (Datry et al., 2014). Whether a channel begins to disconnect from the headwaters, mid-reaches, or downstream (Lake, 2003), fragmentation in intermittent streams creates a mosaic of habitat patches of varying persistence and isolation (Datry et al., 2016). While the fragmentation of intermittent streams can be predictable, the onset, duration, and degree of contraction often is not (Williams, 2006), suggesting considerable potential for variation in habitat quantity, quality, and connectivity over time.

Intermittent streams are highly dynamic, where the wetted habitat quantity can decrease by large proportions by the end of the dry season (Stanley et al., 1997; Jensen et al., 2019) and vary from year-to-year (Allen et al., 2019; Lapides et al., 2021; Moidu et al., 2021). As intermittent streams contract and disconnect, the water quality of the remnant surface water can also change drastically (Acuna et al., 2005; von Schiller et al., 2011). By the end of the dry season, for example, hypoxic conditions are common, and high temperatures can prevail (Lillebo et al., 2007). Connectivity between surface water patches defines the spatial arrangement of habitat (Datry et al., 2016), with distance between pools (Beesley & Prince, 2010) and pool permanence (Bonada et al., 2007) affecting the distribution of species (Jaeger et al., 2014; Rogosch & Olden, 2019; Hedden & Gido, 2020). Habitat quantity, quality, and connectivity shift within and among years in these systems, and are largely dependent on the short- and long-term antecedent precipitation. Both the magnitude and timing of rainfall can control the mosaic of wetted habitats (Costigan at al., 2016), with potential consequences for obligate aquatic and semi-aquatic species (Larned et al., 2010).

Together, surface water quantity, quality, and connectivity define the habitat mosaic of intermittent streams, particularly in systems with distinct cycles of flow cessation, drying, and rewetting (Datry et al., 2017). The relative importance of metacommunity assembly mechanisms varies across these phases (Datry et al., 2016), ultimately driving the abundance and distribution of aquatic species across the landscape. During initial flow cessation, dispersal can act as the dominant control on species composition, whereas during the dry phase, increasingly stressful water quality conditions filter out species with low physiological tolerances (Sarremejane et al., 2017). Upon rewetting, species limited by dispersal constraints can recolonize newly connected habitats, facilitated by key source patches (Magoulick & Kobza, 2003; Ruhi et al., 2017). However, the extent and degree of drying acts as a first-order control on the ability of such ecological processes to shape community structure (Crabot et al., 2019; Sarremejane et al., 2020; Pineda-Morante et al., 2022).

This variability of community assembly mechanisms within intermittent streams is expected to be most pronounced in systems with high seasonal and interannual variability, such as those found in Mediterranean-climate regions, including the Mediterranean Basin and parts of California, South Africa, Australia, and Chile. These climate regions have strong seasonality in precipitation (Gasith & Resh, 1999; Deitch et al., 2017), with wet winters followed by dry summers, as well as high variability in total precipitation across years. This inter- and intra-annual variation leads to differences in the availability of different habitat types within and across years, affecting assemblage dynamics described above, as species and taxa respond variably to the timing, magnitude, and frequency of fragmentation (Sarremejane et al., 2020). While many of these species-specific responses are natural adaptations to seasonal drying, many studies have shown that communities may not be able to recover fully from prolonged drought conditions (Bogan & Lytle, 2011; Driver & Hoeinghaus, 2015), with ultimate consequences for species distribution, habitat partitioning among species and life stages, and recruitment variability.

Given that intermittent streamflow conditions are projected to become increasingly severe (Larned et al., 2010; Pumo et al., 2016; Zipper et al., 2021), often coinciding with critical periods of species' life history (Jaeger et al., 2014), an improved understanding of species' responses to shifting mosaics of wetted habitats within intermittent streams is needed. While many studies have looked at the influence of available wetted habitat on community composition (e.g., Labbe & Fausch, 2000; Bogan & Lytle, 2011; Dexter et al., 2014), most have focused on a gradient of flow intermittency (Bonada et al., 2007; Clarke et al., 2010; Rolls et al., 2016) or a snapshot in time (Mas-Marti et al., 2010; Bogan et al., 2019; Hill & Milner, 2018). Studies that have considered intermittent stream habitat types across time have identified that individual sites can be a 'keystone' for the broader ecosystem, acting as a source and a refuge for invertebrate species (Ruhi et al., 2017). By using a similar framework, we can understand how specific habitat types under the shifting mosaic can support vertebrate species abundance and distribution both within and across years.

The overall goal of this study was to characterize how aquatic species utilize intermittent stream habitats across a wide range of hydrologic conditions in a Mediterranean-climate stream in California (USA). Our specific objectives were to: (1) characterize the variation in the wetted

channel and habitat mosaic within and across years; (2) document aquatic and semi-aquatic vertebrate species presence and characterize the variation in the species abundances across years and in different habitat types; and (3) identify the physical parameters, with a focus on habitat quantity, quality, and connectivity, that explain variation in the abundances of different species and life stages within and across years. To address these objectives, we conducted repeated wet-dry mapping along 5-kilometers of an intermittent stream (Coyote Creek in Santa Clara County, California, USA) over the course of the dry season for 7 years. We also documented the physical characteristics of wetted habitat available in a subset of reaches and surveyed the distribution and abundance of aquatic vertebrate species and one large mollusk species. We examined species and life history stage partitioning between unique habitat types and used linear mixed models to quantify the relative importance of antecedent precipitation and physical and chemical habitat characteristics in determining the abundances of focal species among habitat units and across years.

In particular, we hypothesize that variation in wetted channel will lead to a shifting habitat mosaic that will ultimately control the abundance of aquatic and semi-aquatic vertebrates. We predict that (1) the wetted channel and habitat mosaic will be highly variable both within and across years, with the overall extent and timing of available habitat related to antecedent precipitation but with variable distribution and persistence of wetted habitat; (2) the distribution and abundance of species and life stages will vary depending on the proportion of habitat types within the mosaic; (3) the variation in the distribution and abundance of species and life stages will be driven by habitat size, habitat persistence, and water quality metrics such as temperature and dissolved oxygen.

Methods

Study Site

Coyote Creek (Figure 1a) flows for 102 km through the Diablo Range before draining into the southern San Francisco Bay (Conomos et al., 1985). The 830 km^2 stream basin is underlain by Berryessa Formation shale, Franciscan sandstone, unnamed marine sedimentary rock, and serpentine outcrops (McLaughlin et al., 2002). Several areas contain deep alluvial and colluvial deposits, as well as landslide debris (McLaughlin et al., 2002). The creek runs between the Madrone and Calaveras Faults, and the surrounding area is subjected to mass wasting events, which have deposited large boulders in and around the stream (Witter et al., 2003). The region has a Mediterranean climate, with precipitation typically occurring from October-April, followed by a dry summer season. The average precipitation across the last 30 years (1991-2021) is 535 mm, ranging from 263 mm (2021 Water Year) to 1011 mm (2017 WY) (USGS, 2021). The creek is fragmented by two dams, Coyote Dam and Anderson Dam, downstream from which has managed, perennial flows. Upstream of the upper dam, the creek is naturally intermittent, with flowing reaches that gradually and consistently contract into a series of isolated pools of varying persistence during the summer (Bogan et al. 2019; Figure 1c). Our study site (Figure 1b) is a 5-kilometer, largely unimpacted, section located in Henry Coe State Park. The basin and surrounding area are the ancestral homelands of the Amah Mutsun Tribal Band, who are the original stewards of the land.
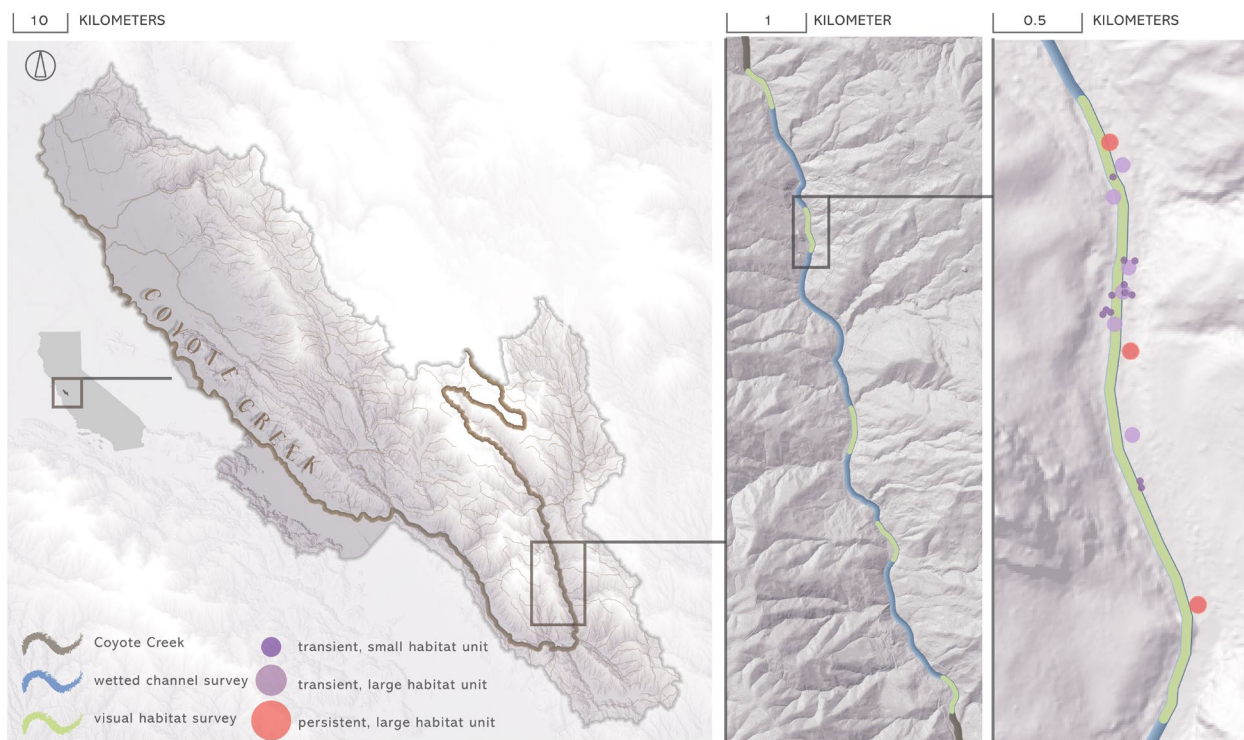
Figure 1. Map showing (a) the location of our 5-kilometer study site; (b) the distribution of the 250-meter reaches where we assessed habitat and surveyed aquatic vertebrates; and (c) an example from August 2018 of the types and distribution of habitat units sampled. 'Persistent, large' habitat units remained wetted across all years regardless of antecedent precipitation, while 'transient, small' and 'transient, large' habitat units dried in some years (see Methods)

Wetted Channel Surveys

We conducted surveys of wetted habitat conditions from 2014 to 2021 (except 2020, due to Covid-19 restrictions) along the 5-kilometer study reach in Coyote Creek (Figure 1b). In 2014, we surveyed at the end of the dry season (i.e., September; Bogan et al. 2019). Beginning in 2015, we expanded the study to include monthly surveys from the onset of disconnection (typically July or August) through the end of the dry season (i.e., until the first autumn rainfall, typically October or November). The timespan within which surveys were conducted encompassed extreme low (2021: 263 mm) and high (2017: 1011 mm) precipitation years, including the final years of a statewide multi-year drought between 2012-2016, capturing the wide range of interannual hydrologic variability observed in the system.

Between 2014-2016, monthly wet-dry mapping surveys were conducted by field crews walking the channel with a handheld Garmin eTrex GPS unit (+/- 15 m accuracy) and recording the coordinates at every point of surface water disconnection and reconnection along the channel. Disconnected reaches were defined as portions of the stream channel where there was a break in continuous surface water connectivity, with surface water patches being at least 1 m in length and > 0.10 meters deep. These coordinates were then used to digitize a streamline in ArcGIS 10.7.1

representing wet and dry reaches at each survey. Between 2017-2021, surveys were conducted by field crews using a Bad Elf GPS (+/- 1 m accuracy) connected to ArcCollector 21.0.4 on a tablet, using the same methods to map the presence of surface water. This latter method automatically digitizes and georeferences the wet and dry reaches along the stream. We used these data to create monthly maps of wetted habitat conditions across all years of the study.

Habitat and Biological Surveys

Along our 5-kilometer study stretch where we conducted wet-dry mapping, we identified five representative 250-meter reaches for more intensive habitat and biological sampling (Figure 1b). We conducted habitat and biological surveys for each wetted habitat unit within each 250-meter reach. A wetted habitat unit was defined as any disconnected surface water patch, which included both flowing reaches and isolated pools, with an area greater than 30 cm^2. This size threshold was chosen as habitat patches smaller than 30 cm^2 were unlikely to support aquatic vertebrate species. For each wetted habitat unit, presence and abundances of vertebrates were estimated using a rapid assessment approach, in which species abundance was estimated by visually scanning the wetted habitat unit for amphibians, reptiles, and fishes in the water column (see the complete taxa list on Table 1). Water clarity in Coyote Creek is generally high during the dry season, and species can be identified at depths of 2 m (Bogan et al., 2019). We also documented abundances of California floater mussels (*Anodonta californiensis*) because they are large (up to 12cm), have a life stage dependent upon freshwater fishes, and are of conservation concern. In addition to the visual assessment, we conducted spot sampling in undercut areas and along the benthos using a dip-net to identify benthic-oriented vertebrates. Each species observed was grouped into one of five abundance classes for analyses based on visual estimation: 1-10; 11-100; 101-500; 501-1000; >1000 individuals. Visual estimation of abundance was completed by two observers (typically RAL and SMC). We distinguished between juvenile and adult life stages for some amphibians (*Rana draytonii,* red-legged frog; *Rana boylii,* yellow-legged frog) and fish (*Hesperoleucus venustus,* coastal roach; *Catostomus occidentalis,* Sacramento sucker; *Ptychocheilus grandis,* Sacramento pikeminnow). To standardize sampling effort among the units, the time spent sampling was proportional to the surface area of the habitat unit.

For each wetted habitat unit, we collected and compiled a suite of metrics that relate to habitat suitability, including measures of quantity, quality, and connectivity. We measured the *maximum length*, *maximum width*, and *maximum depth* of each wetted habitat unit as habitat quantity metrics. We also calculated a series of connectivity measures for each habitat unit. These include *distance to nearest patch,* which is the Euclidean distance from the focal habitat unit to the nearest habitat unit, and *distance to permanent pool,* which is the Euclidean distance from the focal unit to the nearest permanent pool, which are a subset of pools that persisted during the driest conditions surveyed. *Distance-weighted area* was calculated as the distance to the nearest wetted habitat unit, divided by the area of the focal habitat unit. To characterize the long-term *wetted persistence* of the focal unit, we calculated the proportion of years in which the focal habitat unit had surface water in the month of September. Beginning in 2017, we additionally measured several physicochemical parameters, including *water temperature, dissolved oxygen, pH,* and *conductivity* at each wetted habitat unit.

Habitat Mosaic Characterization and Species Utilization

We characterized habitat units based on their size, degree of persistence, and connectivity. We used a k-means clustering approach (factoextra 1.0.7 package; Kassambara et al., 2017) to identify three habitat types based on their *depth, wetted persistence, distance to nearest patch,* and *distance-weighted area*. We additionally tested clustering with the inclusion of *temperature, dissolved oxygen, conductivity,* and *pH* to the aforementioned variables to determine whether such variables affected clustering. However, these water quality variables were not included in the final clustering approach, as they were not measured for wetted habitat units sampled prior to 2017. Three clusters were chosen as the optimal number that yielded distinct classes without overfitting. We summarized the proportion of wetted habitat units that fell into each class both within and across years to understand the shifting distribution of habitat types at short- and long-term timescales. We used ANOVAs (aov function in R 4.0.2; R Core Team, 2022) to further determine if there was a difference in the distribution of habitat types among years and in the abundances of species and stages in different habitat unit types. We used PERMANOVA with Gower distance (vegan package in R 4.0.2; Oskanen et al., 2013) to determine whether community composition was different among habitat types. Abundances were determined by transforming the abundance classes into ordinal levels (e.g. abundance class of 1-10 became level 1; 11-100 became level 2; 101-500 became level 3, and so on) for each species surveyed at each habitat unit.

Evaluating Species Distribution and Abundance

Next, we used linear mixed models (lme4 1.1-29 package; Kuznetsova et al., 2017) to explore the influence of specific habitat characteristics on the abundances of different vertebrate species within and across years. Two models were developed: one evaluating the effects of physical variables and the other evaluating the effects of both physical and water quality variables, with year and month as random variables for both. The physical model included data from all years (2014-2019, 2021) of the study. A separate model was developed for the water quality model, since physicochemical parameters were measured only in 2017-2019 and 2021, and thus included only those years. For the physical model, only species that occurred in >10% of the habitat units were included due to insufficient occurrence data to analyze rare species. The species meeting this criterion for the physical habitat models included Ohlone sculpin (*Cottus ohlone ohlone)*, sucker, coastal roach, pikeminnow, yellow-legged frog, and red-legged frog. The species meeting the 10% criterion for the water quality models included sculpin, pikeminnow, roach, and sucker. We developed separate models for species in which both juvenile and adult abundance was estimated (red-legged frog, yellow-legged frog, pikeminnow, sucker, roach). The abundance classes were transformed into ordinal levels (described above) and used as the response variable for each species and stage.

For the physical models, we evaluated the influence of several variables on species abundances, including *depth, distance to nearest patch, distance-weighted area, distance to permanent pool*, and *wetted persistence* (all described above). Additionally, we included variables that captured the influence of short- and long-term climate. We included *days since last rainfall* to evaluate the influence of the timing of most recent precipitation and *spring precipitation* (sum of total March,

April, and May precipitation for the watershed), to evaluate the influence of the seasonal and interannual variation in precipitation on focal species. Both climate factors were calculated using PRISM climate data (Daly et al., 2008). For the water quality models, we additionally included the following physicochemical variables: *water temperature* (°C), *dissolved oxygen* (%), *pH*, and *conductivity* (uS/cm). For all models, year and month were included as random effects (see Table S1 for full summary of model variables). To understand how species' abundances varied within and across years, the influence of the random effects was tested with likelihoods ratio tests (Zuur et al., 2009) using the lme4 1.1-29 package (Kuznetsova et al., 2017), which compared models with the full set of variables with nested models without the random effects.

Results

Variation in the Wetted Channel and Habitat Mosaic

Wetted channel surveys showed variation in both the onset and degree of fragmentation across years (Figure 2a), with contraction patterns largely following patterns of precipitation. For example, in the wettest year surveyed (2017), fragmentation did not occur until September, when wetted habitat contracted by 35%. In contrast, in the driest year surveyed (2021), wetted habitat had contracted 89% by September. The pattern of drying typically began with initial disconnection of a few riffles, and gradually expanded over the course of the summer. Comparing wetted conditions in September across years, we found that some reaches were consistently more likely to retain surface water than others (Figure 2b). This variation in wetted persistence can be seen in the distribution and length of wetted lengths across time (Figure S1). For example, in September 2018, 24% of the channel was wetted, while in August 2016, 25% of the channel remained wetted. Despite these similar proportions, the spatial distribution of wetted lengths were nearly opposite. Similarly, the proportion of wetted channel in June 2021 and September 2019 were comparable, at 43% and 47% respectively, but the connected wetted lengths were very different across the two surveys. The former consisted of several short, disconnected patches, whereas the latter contained longer, connected wetted lengths. We observed that several persistent, wetted regions were associated with springs, seeps, and scour-forming features such as boulders and bedrock (Figure S2).
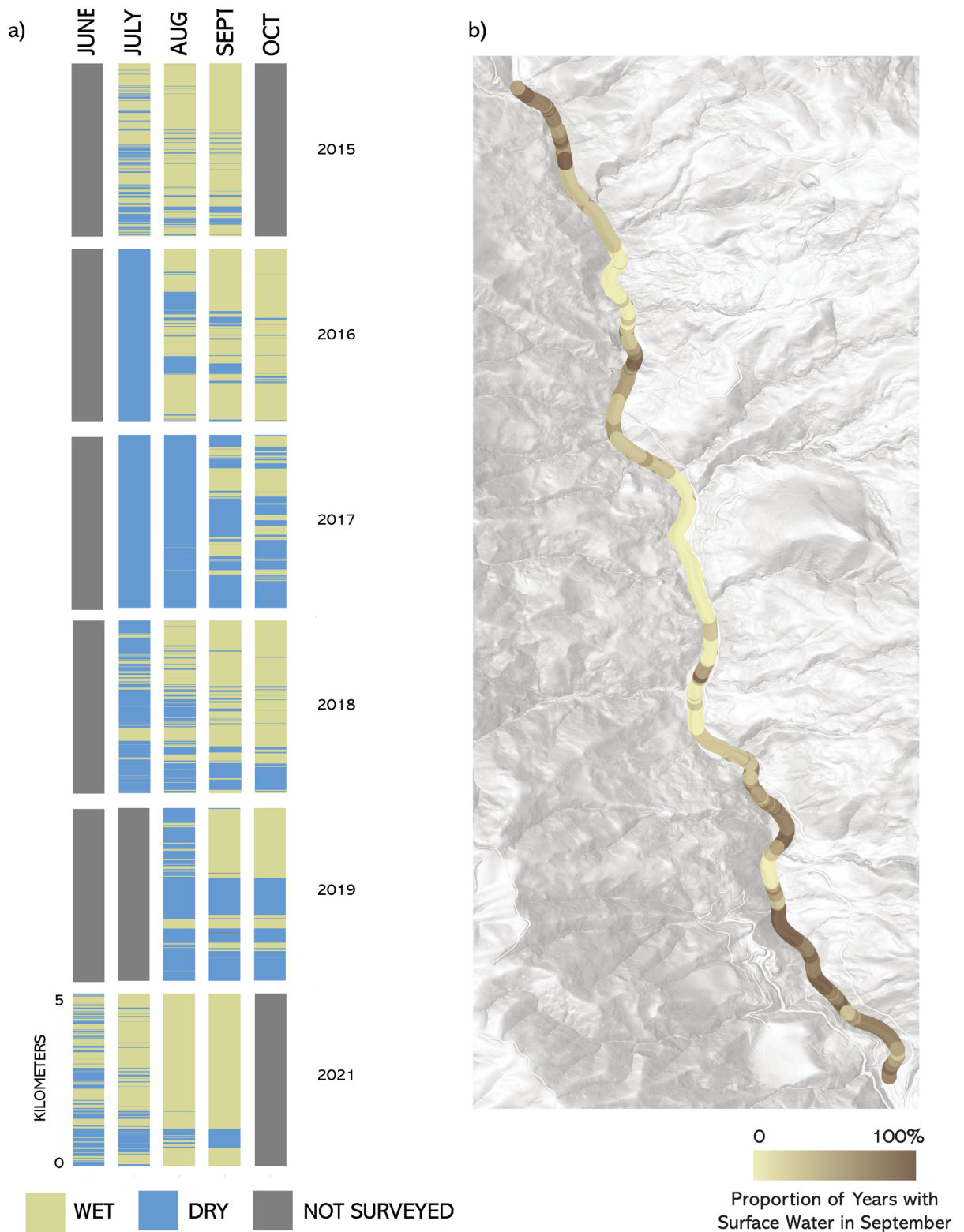
Figure 2. (a) Spatial distribution of wetted habitat along our 5-kilometer study site across the sampled summer months from 2015-2021; (b) The proportion of years with surface water in September across 2015-2021

Results from the k-means clustering yielded 3 distinct clusters (Figure S3), which were consistent when determined through only physical variables, as well as determined through physical and water quality variables. Thus, since water quality variables were not measured prior to 2017, the clustering approach using only physical variables was applied. The physical and water quality characteristics varied between the three clusters (Figure S4), with distinct distributions of habitat quantity, quality, and connectivity associated with each. Using the mean value of the clustering variables for each class (Table S2), we identified ecological characteristics that defined and classified each cluster. Cluster A was typified by wetted habitat units with a high degree of wetted persistence (mean: 91%) and greater maximum depth (mean: 1.19m). Cluster B contained wetted habitat units that were moderately persistent (mean: 48%) but still deep (mean: 0.77m). Cluster C contained wetted habitat units that were not persistent (mean: 26%), and shallow (mean: 0.24m). In terms of degree of connectivity, Cluster B was further from nearby habitat units than Cluster A or Cluster C. Thus, we described the three clusters based on their dominant characteristics, where wetted habitat units in Cluster A are more likely to be "persistent, large", units in Cluster B to be "transient, large", and units in Cluster C to be "transient, small".

Results from ANOVA tests showed a significant difference (p < 0.001) in the proportion of habitat unit types present between years. In wet years, such as 2017, there was a lower number of total isolated habitat units, as much of the channel remained wetted across the summer and many riffles retained flowing water through the dry season (Figure 3a; 3d). However, during a moderate year, such as 2018, the number of isolated habitat units within the mosaic increased, and included transient habitat units that varied in size and duration of persistence, as well as persistent habitat units (Figure 3a; 3c). Some of the large transient habitat units remained wetted throughout the summer, whereas some of the smaller transient habitat units that were sampled in the early summer were dry by late summer. During dry years, such as 2021, much of the channel went dry, with the only available wetted habitat consisting of large persistent units, like those illustrated in Figure 3e. While the total number of habitat units present in wet years and in dry years were comparable (Figure 3a), the difference in mean wetted area demonstrates the differences in available habitat under different antecedent precipitation conditions.

Species Presence and Abundances Across Years

Results from our visual surveys of vertebrates revealed a diverse assemblage of aquatic and semi-aquatic species in Coyote Creek across multiple years of study (Table 1). While the overall assemblage was generally stable through the study period, the relative abundances of individual species varied across years (Figure 4), often also differing among habitat unit types ('transient, small', 'transient, large', and 'persistent, large') for some species. Results from the PERMANOVA analysis indicated that there was a significant difference in the community composition across habitat types.

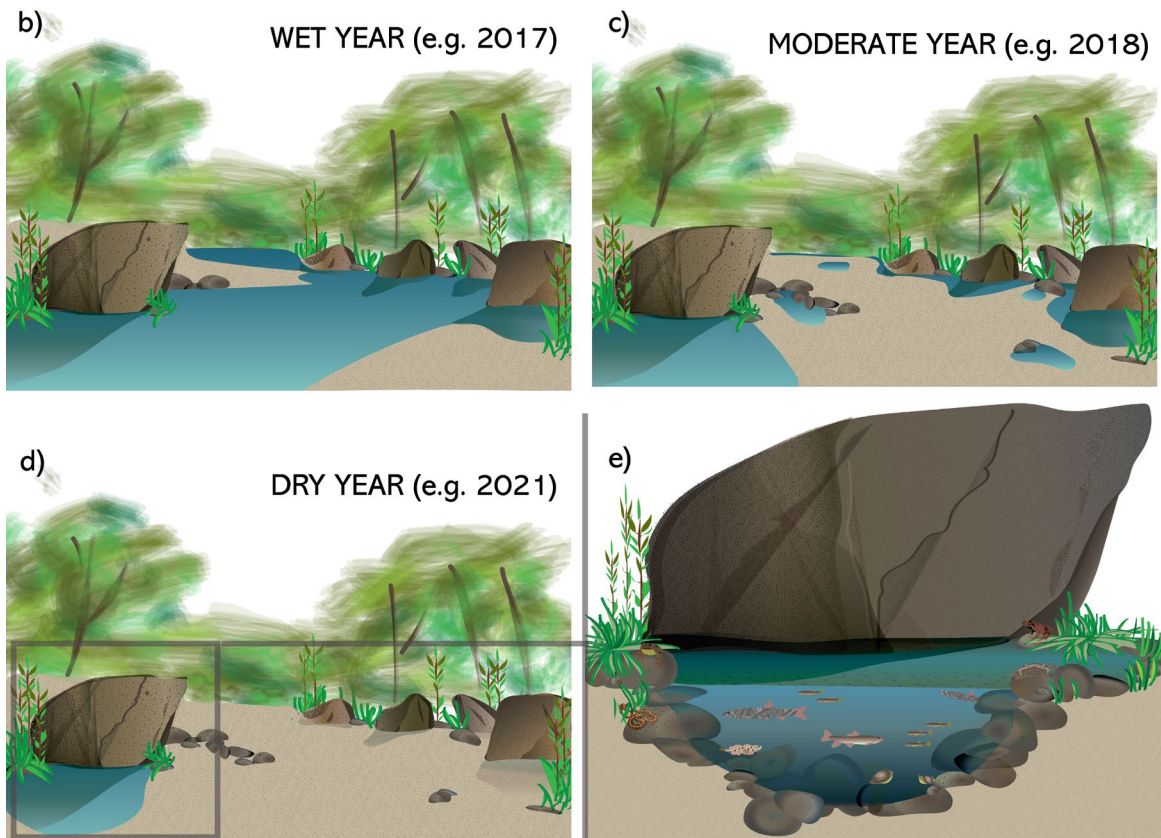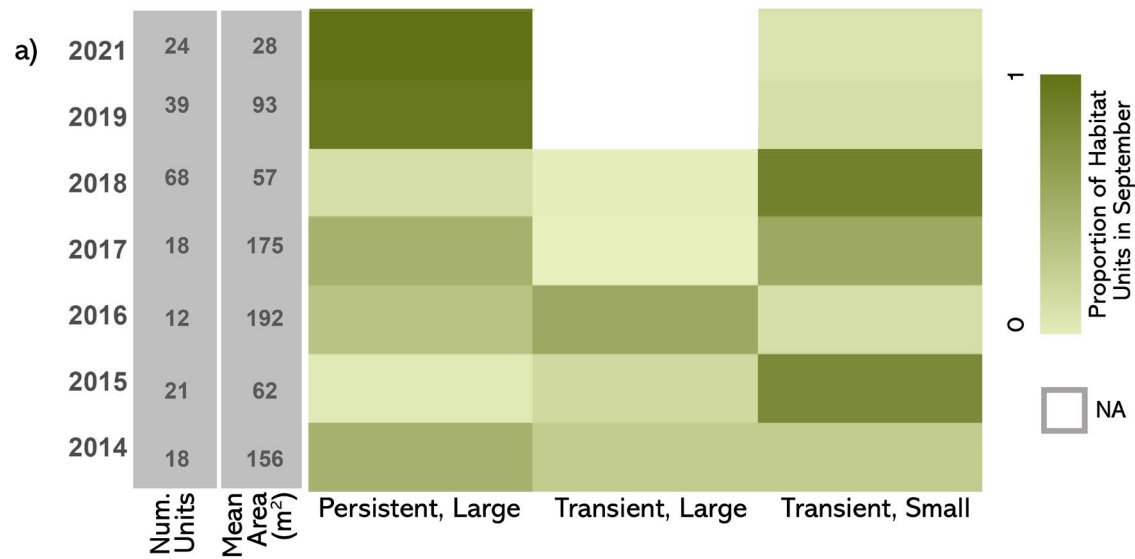|	Num. Units	Mean Area (m²)	Persistent, Large	Transient, Large	Transient, Small
2021	24	28			
2019	39	93			
2018	68	57			
2017	18	175			
2016	12	192			
2015	21	62			
2014	18	156			

Figure 3. The habitat mosaic of an intermittent stream over a range of annual precipitation conditions: (a) the total number, mean area, and proportion of different habitat unit types during September of each sample year; (b) during a wet year, the stream is largely connected with flowing riffles and few isolated habitat units; (c) during a moderate year, the stream contracts to several isolated habitat units and retains some surface connection, with some of these habitat units drying by the end of the summer; (d) during a dry year, the stream contracts to a few, large, persistent habitat units; and (e) in dry years, persistent habitat units are the only habitat available for aquatic vertebrates

Taxonomic Group	Native / non-native	Species Name	Common Name
Fish	Native	*Hesperoleucus venustus*	Coastal roach
		Catostomus occidentalis	Sacramento sucker
		Ptychocheilus grandis	Sacramento pikeminnow
		Cottus ohlone ohlone	Ohlone sculpin
		Lampetra sp.	Non-parasitic brook lamprey
		Oncorhynchus mykiss	Rainbow trout
	Non-native	*Micropterus salmoides*	Largemouth bass
		Lepomis macrochirus	Bluegill sunfish
Amphibians	Native	*Rana boylii*	Foothill yellow-legged frog
		Rana draytonii	Red-legged frog
		Pseudacris sierra	Sierran treefrog
		Anaxyrus boreas halophilus	California toad
		Taricha torosa	California newt
	Non-native	*Lithobates catesbeianus*	American bullfrog
Reptiles	Native	*Actinemys marmorata / pallida**	Northwestern and Southwestern pond turtles
		Thamnophis atratus zaxanthus	Diablo Range garter snake
Mollusk	Native	*Anodonta californiensis*	California floater mussel

Table 1. Summary of species observed during visual surveys of Coyote Creek

*these two species overlap at our site, may be admixed, and are not easily distinguished visually

Large-bodied adult fish were most likely to be observed in persistent habitat units, with 83% of observations of adult pikeminnow and 70% of adult sucker associated with habitat units that rarely or never dried during our study period (Figure 4). In contrast, some species or stages were found in greater numbers in transient habitat units. For example, 76% of juvenile roach and 70% of sculpin (juveniles and adults combined) observations were associated with habitat units that dry during some years. Further, 24% of the transient, small habitat units were occupied exclusively by juvenile roach. Juvenile roach was the only species and stage to be predominantly found exclusively in these habitats. In contrast, only 1% and 0.2% of transient, small habitat units contained only sculpin and adult roach, respectively. Pikeminnow and sucker were only found in shallow habitat units when at least one other species was present (i.e., they were never exclusive users of transient, small habitat units).
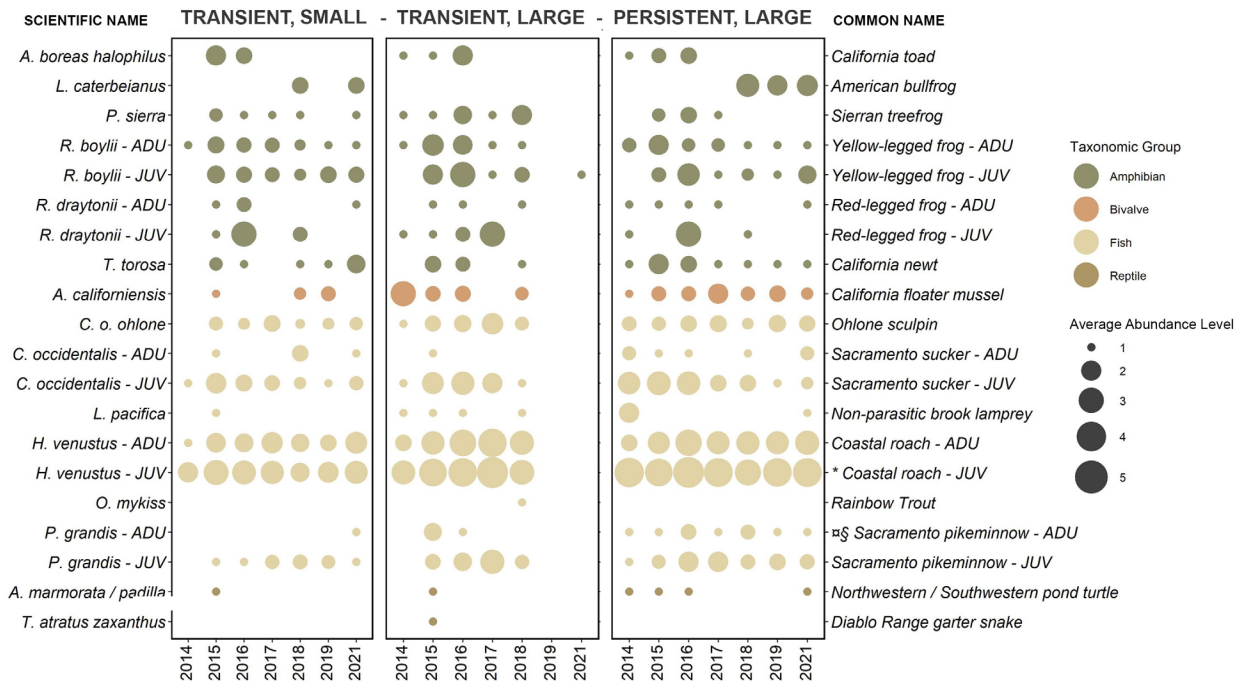
Figure 4. Cumulative species presence and average abundance level across years in 'transient, small' habitat units, 'transient, large' habitat units, and 'persistent, large' habitat units from 2014-2021. Abundance levels were determined by transforming the abundance classes into ordinal levels (e.g. abundance class of 1-10 became level 1; 11-100 became level 2; 101-500 became level 3, and so on) for each species surveyed at each habitat unit. The symbol * precedes the common name of species that had a significantly different distribution between the small and large transient habitat units ($p < 0.05$); ¤ denotes a significantly different distribution between transient, small and persistent, large habitat units ($p < 0.05$); § denotes a significantly different distribution between transient, large and persistent, large habitat units ($p < 0.05$). JUV – juveniles; ADU – adults.

Influence of Habitat Quantity, Quality, and Connectivity on Species' Abundances

The abundances of different species and life stages present in individual habitat units were explained by indicators of habitat quantity, quality, and connectivity, but to varying degrees (Table 2). For example, *depth* (one of the habitat quantity metrics) was significant for nearly all species and stages, except for juvenile yellow-legged frogs. Habitat connectivity was also important in explaining the abundances of several species. For example, *distance to the nearest patch* or *distance-weighted area* were significant for all species and stages except adult suckers, adult pikeminnow, and red-legged frogs. The *distance to permanent pool* variable was significant for roach, juvenile yellow-legged frogs, and adult red-legged frogs, while the *wetted channel persistence* variable was significant in explaining the abundances of adult sucker, adult pikeminnow, and adult yellow-legged frogs. Climate variables representing the magnitude and timing of spring precipitation were also important for some species. The *days since rain* variable was significant for sculpin, adult roach, juvenile pikeminnow, and juvenile red-legged frogs,

while the *spring precipitation* variable was significant for adult roach. Results from the likelihood ratio tests indicate that for all species and stages (except for adult roach, adult yellow-legged frog, and adult red-legged frog), year had a greater importance than month in explaining abundances.

When water quality variables (temperature, dissolved oxygen, pH, and conductivity) were included in our models for the years 2017-2021, we found that physical variables remained significant for all species and stages, particularly *depth* (Table 3). *Water temperature* and *pH* was also significant in explaining the abundance of juvenile roach and adult pikeminnow, while *dissolved oxygen* was significant in explaining the abundance of both stages of roach, suggesting that water quality also played a role in determining patterns of use and abundance.

Species	Depth	Distance to Nearest Patch	Distance - Weighted Area	Distance to Permanent Pool	Wetted Channel Persistence	Days Since Rain	Spring Precip-itation	Year †	Month †	R² - Marginal	R² - Cond-itional
C. o. ohlone	**	***	***			**		***		0.27	0.35
C. occidentalis - Adu	***				*					0.12	0.16
C. occidentalis - Juv	***	*						***	•	0.12	0.61
H. venustus – Adu	***	***	***	•		***	•		*	0.58	0.59
H. venustus - Juv	***	***	***	*				***	**	0.54	0.62
P. grandis - Adu	***				**					0.32	0.32
P. grandis - Juv	***	**	**			•				0.42	0.45
R. boylii - Adu	*		•		*			**	**	0.12	0.35
R. boylii - Juv		***	***	*				***	*	0.11	0.25
R. draytonii - Adu	*			*						0.06	0.29
R. draytonii - Juv	•					*				0.13	0.15

Table 2. Results from the species abundance and distribution linear mixed models for each individual species and stage. Variables with a '†' symbol were included in the model as random effects, and were evaluated using likelihood ratio tests. Significance levels are as follows: <0.001 '***' 0.001 '**' 0.01 '*' 0.05 '•'

Species	Temp (°C)	Dissolved Oxygen (%)	pH	Conductivity (uS/cm)	Depth	Dist to Nearest Patch	Dist Weighted Area	Dist to Perm Pool	Persistence	Days Since Rain	Spring Precip	Year	Month	R² – Marginal	R² – Conditional
C. o. ohlone					***	***	***		**			*		0.28	0.32
C. occidentalis - Adu					*			•						0.06	0.06
C. occidentalis - Juv					***	•	•	•		*		***		0.14	0.36
H. venustus - Adu		*			***	***	***			**				0.59	0.62
H. venustus - Juv	**	***	•		***	***	***			***		**		0.59	0.63
P. grandis - Adu	•		***		***	*	*	*	•					0.30	0.32
P. grandis - Juv				•	***	**	**				*			0.39	0.39

Table 3. Results from the physicochemical linear mixed models for each individual species and stage. Significance levels are as follows: <0.001 '***' 0.001 '**' 0.01 '*' 0.05 '•'

Discussion

Our results show that intermittent streams can be characterized as shifting habitat mosaics that support unique species and life stages across space and time and play an important role in maintaining regional aquatic biodiversity. We found that available wetted habitat varied considerably across the summer dry-down period and across years with different patterns of antecedent precipitation, with wet years exhibiting a drastically different trajectory and mosaic of habitat types than moderate and dry years. Species' abundances were primarily influenced by habitat quantity and connectivity. Our results indicate that some species and life stages, such as adult pikeminnow and adult sucker, were consistently found in persistent, large habitat units, whereas others, such as roach, were found in all types of habitats, including small and large transient habitat units.

Ecological consequences of habitat persistence and connectivity

Spatial and temporal variation in fragmentation has distinct implications for community assemblage mechanisms. While many species have developed resistance and resilience strategies in overcoming seasonal fragmentation, unprecedented loss of hydrologic connectivity via supra-seasonal drying events (Lake, 2003) or climate change (Jaeger et al., 2014) can challenge

successful community recovery. Under such conditions, dispersal is limited as habitats become more isolated, and key source habitats are increasingly relevant in sustaining diversity (Mouquet & Loreau, 2003; Ruhi et al., 2017). At our site, we observed the habitat mosaic of Coyote Creek shift both within and across years, with surface water presence at the end of particularly dry years being constrained to a small number of persistent habitat units. The variability of the wetted extent across years had strong ecological consequences, and we observed a diverse assemblage of native species using the available wetted habitat in wet and dry years. An earlier study from this site reported that a subset of habitat units persisted during extreme drought conditions of 2014 and provided refuge for a suite of native vertebrates and invertebrates (Bogan et al. 2019). Our results from 2014-2021 provide further evidence that several species depend on these persistent habitat units, including adult pikeminnow, adult sucker, and adult yellow-legged frogs. Beesley & Prince (2010) similarly found that pool persistence was positively correlated with aquatic species richness, and Labbe & Fausch (2000) found that stable pools played a critical ecological role in facilitating higher rates of survival for fishes, especially for older individuals. Such refugial habitats are thought to be preferred by and critical for supporting large-bodied fish; in a study focusing on large-bodied fish in an Australian intermittent river, Marshall et al. (2016) showed that most individuals returned to their original persistent pool after flow events. Indeed, at our site, large, stable pools are particularly important for large-bodied fish like adult pikeminnow (>60 cm length at our site) that are unlikely to survive in transient, small habitat units.

While persistent habitat units were reliably present even in the driest years, we observed wetted habitats of varying size and connectivity under moderate conditions. We found that the abundances of fishes increased with decreasing distance to the nearest habitat unit. Isolated patches are more likely to have been disconnected for longer and may have poorer water quality and shrinking habitat availability as a result; Obedzinski et al. (2018) suggested that the onset of pool disconnection indicated a shift in water quality of habitats, and found that days since disconnection was a significant control on fish survival in intermittent streams. We further found that most vertebrates at our sites preferred larger and more connected habitat patches. Similarly, Taylor (1997) found that both stream pool volume and connectivity positively influenced fish species richness, with the effect varying between species. Driver & Hoeinghaus (2016) also reported that larger pools with greater connectivity offered higher quality refugia and held a greater number of species. Two exceptions to this general pattern for fish in our study were adult pikeminnow and adult sucker, both of which were not influenced by connectivity metrics. These large-bodied fish are highly dependent on persistent habitat units and are therefore less influenced by the characteristics of neighboring habitat units. In small Mediterranean stream, Aparicio & De Sostoa (1999) also found that adult fish were highly sedentary and seasonally stable, with individuals occupying deeper sections being less mobile than those found in shallower reaches.

Evidence of long-term drought resistance, vulnerability, and invasion

Despite the multi-year drought from 2012-2016, many species showed remarkable resistance to harsh conditions. In October 2014, the stream had contracted to a small number of remnant pools (Bogan et al. 2019), yet several species were widely distributed across subsequent drought and non-drought years, including roach, sculpin, pikeminnow, California newts, and California toads. Roach appear to be the most resistant and resilient species in the assemblage. They were ubiquitous across all years of study and were found in both persistent habitat units and shallow habitat units with high temperatures and low dissolved oxygen. Similar habitat use by roach was found by Moyle & Nichols (1973), and they suggested that low oxygen levels in pools likely excluded other native species. Since these marginal habitats are most likely to host juvenile roach, they may play an important role in the recruitment success of roach, particularly in wetter years when many small habitat units persist through the dry season. Although native inland fishes of California have many adaptations for withstanding and recovering from long-term drought, Moyle & Nichols (1974) warned that even species that are currently ubiquitous should be monitored closely. Climate models predict more frequent and prolonged drought conditions in California (Diffenbaugh et al., 2015; Swain et al., 2018), which, in this system, may result in elimination of the small habitat units used exclusively by roach.

Other species were more sensitive to drought conditions, including pond turtles and Sacramento sucker. We previously observed a die-off of pond turtles during extreme drought conditions in 2014 (Leidy et al., 2016), which was likely a consequence of a series of dry years with unfavorable conditions. We observed very few pond turtles from 2015-2021, indicating the die-off may have had long-term, population-level consequences. In our observations, Sacramento suckers were common in persistent habitat units in 2014, but rare in 2015-2021. Because adult suckers tend to prefer large habitat units or flowing waters (Moyle & Nichols, 1973) and successful reproduction and robust year classes are more likely after wet years (Moyle, 2002), multiple consecutive dry years in the last decade have likely reduced the survival, reproduction, and recruitment of this species in Coyote Creek. Given these constraints, local extirpations of sensitive fish species may occur from consecutive drought years, with a limited chance to renew population sizes (Moyle & Nichols, 1974).

Beyond the impacts of extended drought on native vertebrates, we also observed the establishment of nonnative bullfrogs over the course of our study. While bullfrogs are known to occur in the Coyote Creek watershed, they were not detected in the study area in from 2014-2016. However, we detected a small number of bullfrogs in 2017 that have since become more widespread, likely due to a particular sequence of wet and dry years (Kupferberg et al., 2021). Initial bullfrog presence followed the wet winter of 2017, where higher flows prevented tadpole desiccation in the summer and fall (Kupferberg et al., 2021), while subsequent lower precipitation years prevented winter scouring and facilitated range expansion of this more lentic species (Kupferberg, 1996). The establishment of bullfrogs in the system is expected to have deleterious impacts on native amphibian populations (Moyle, 1973; Kupferberg, 1997; Lawler et al., 1998), particularly in persistent pools with concentrated food resources (Kiesecker et al., 2001). In our study, 42% of habitat units containing native red-legged frogs were within 100

meters of a habitat unit containing bullfrogs, well within the dispersal ability of bullfrogs (Kahrs, 2006), increasing the risk of native species displacement.

We also noted a few occurrences of non-native fishes, such as largemouth bass (*Micropterus salmoides)* and bluegill sunfish (*Lepomis macrochirus)*, but only as isolated individuals. These species were likely washed into the creek from small upslope impoundments (stock ponds), and the individuals were not seen in subsequent surveys. Many studies have shown that disturbance from prolonged drought can create conditions that facilitate the establishment of opportunistic invasive species (Bernardo et al., 2003; Rahel & Olden, 2008; Beche et al., 2009; Diez et al., 2012). But the opposite pattern has also been observed, supporting the environmental resistance hypothesis, where abiotic controls such as highly variable flow regimes, prohibit invasion (Baltz & Moyle, 1993). This has been observed at our site and more broadly, where native stream fishes may be better adapted to withstand drought conditions in intermittent streams compared to non-native species (Closs & Lake, 1996; Ostrand & Wilde, 2011; Driver & Hoeinghaus, 2016).

The role of shifting habitat mosaics in supporting different species and life stages

Our results indicate three main typologies of within the over-summer habitat mosaic: 'transient, small' and 'transient, large' habitat units that are sensitive to antecedent rainfall, and 'persistent, large' habitat units that are reliably wetted even through the driest conditions. Previous studies have considered intermittent stream habitats based on gradients of permanence (Bonada et al., 2007; Beesley & Prince, 2010), distance to permanent water (Davey & Kelly, 2007), and pool depth (Magoulick, 2000; Dekar & Magoulick, 2007). Our results confirm the conservation relevance of categorizing intermittent stream habitats based on their physical, temporal, and spatial characteristics. Here, we reveal the importance of transient pools – small pools that can persist following wet winters but not under drier conditions – and further emphasizes how the habitat mosaic itself is affected by antecedent conditions, with likely consequences for the species and size classes that benefit from these shifting habitats. In general, we found habitat unit size (measured as *maximum depth*) to be the most important variable in predicting the distribution and abundance of most species, and that deep, persistent habitat units host a diverse assemblage of native species. Adult and large-bodied fish were particularly prevalent in these persistent habitat units, while shallow habitats were exclusively and ubiquitously used by juvenile roach, suggesting that they may be excluded from other habitats by predators or competitors. Previous work has noted such patterns, with persistent pools hosting large predatory fish while small minnows were restricted to spatially isolated, shallow habitats (Capone & Kushlan, 1991). In intermittent streams where riffles rarely persist through the summer, this could cause less-dominant species to be stranded in suboptimal habitats (Woelfle-Erskine et al., 2017). Roach may be similar to other fish species with broad water quality tolerances, whose abundances are largely controlled by the presence of water instead of specific water quality conditions (Matthews, 1987; Elliott, 1999; Labbe & Fausch, 2000). Indeed, Labbe & Fausch (2000) found that despite seemingly uninhabitable conditions, marginal patches often acted as rearing habitats for young-of-year. In our study system, juvenile roach were predominantly found in shallow habitat units, providing possible evidence for life history partitioning. Intermittent streams have been noted to

provide differential habitats for separate life stages of fishes (Pease et al., 2006; Archdeacon & Reale, 2020), and the distribution of life stages between persistent habitat units and transient habitat units in our study supports this idea.

The differentiation of habitat use between units that vary in size and persistence becomes an important consideration when considering the future impacts of climate change. Given projections of increasing duration and intensity of drought conditions (Diffenbaugh et al., 2015; Swain et al., 2018), it is likely that some intermittent systems may lose the transient, small habitat units that are currently common during the summer dry-down. The loss of that type of habitat could have consequences for population dynamics of many species of fishes. Roach have exhibited striking ability to survive in habitats with high temperatures and low oxygen (Cech et al., 1990), and given their widespread distribution in our system, are likely to have high colonization and low extinction rates (Whitney et al., 2016). However, if supra-seasonal droughts limit the number of habitat refuges available to species like roach, it can lead to recruitment failure and catastrophic mortalities (Archdeacon et al., 2020). Large, persistent habitat units sustain populations of adult fish that are rarely found in shallow habitat units, and act as the only refuge for all species during severe dry conditions. These unique sites can be considered 'keystone' habitats (Ruhi et al., 2017), as they may disproportionally support regional biodiversity during extreme drought. Such habitats are of conservation interest, and can be prioritized during management decision making.

Conclusion

Results from our multi-year study shed light on the long-term patterns of species distributions and abundance. We documented a high variability in the habitat mosaic both within and across years in Coyote Creek, with consequences for the vertebrate assemblage. Our 7-year study encompassed extreme high and extreme low rainfall years, including the wettest and driest years in recent history. Our results emphasize strong inter-annual variation in the abundances of aquatic vertebrates, and emphasize the importance of habitat quantity, quality, and connectivity in influencing distributions, abundance, and patterns of invasion. While all native vertebrate species persisted through prolonged drought, we observed species-specific changes in distribution and abundances. We found a different assemblage in large, isolated but persistent habitat units (including adult pikeminnow and suckers) versus small, closely-linked patches (which were dominated by juvenile roach). Given projections for increased climate variability and extreme conditions, special management consideration must be given to systems such as these, which support diverse but vulnerable assemblages of native vertebrate taxa during drought conditions.

Acknowledgements

Supplementary Information

Variable	Description	Years Measured	Physical Model	Water Quality Model
Depth	Maximum depth of the focal habitat unit	2014-2019, 2021	X	X
Distance to nearest patch	Euclidean distance from the focal habitat unit to the nearest habitat unit	2014-2019, 2021	X	X
Distance-weighted area	Euclidean distance to the nearest wetted habitat unit, divided by the area of the focal habitat unit	2014-2019, 2021	X	X
Distance to permanent pool	Euclidean distance from the focal unit to the nearest permanent pool, which are a subset of pools that persisted during the driest conditions surveyed	2014-2019, 2021	X	X
Persistence	Proportion of years in which the focal habitat unit had surface water in the month of September	2014-2019, 2021	X	X
Days since last rainfall	Number of days since previous precipitation event	2014-2019, 2021	X	X
Spring precipitation	Sum of total March, April, and May precipitation for the watershed	2014-2019, 2021	X	X
Water temperature	Water temperature (°C), measured using a YSI ProQuatro Handheld Multiparameter Meter	2017-2019, 2021		X
Dissolved oxygen	Dissolved oxygen (%), measured using a YSI ProQuatro Handheld Multiparameter Meter	2017-2019, 2021		X
pH	pH, measured using a YSI ProQuatro Handheld Multiparameter Meter	2017-2019, 2021		X
Conductivity	Conductivity (uS/cm) , measured using a YSI ProQuatro Handheld Multiparameter Meter	2017-2019, 2021		X
Year	Sampling year; included as random effect	2014-2019, 2021	X	X
Month	Sampling month; included as Random effect	2014-2019, 2021	X	X

Table S1. Summary of the variables included in the species abundance and distribution linear mixed models
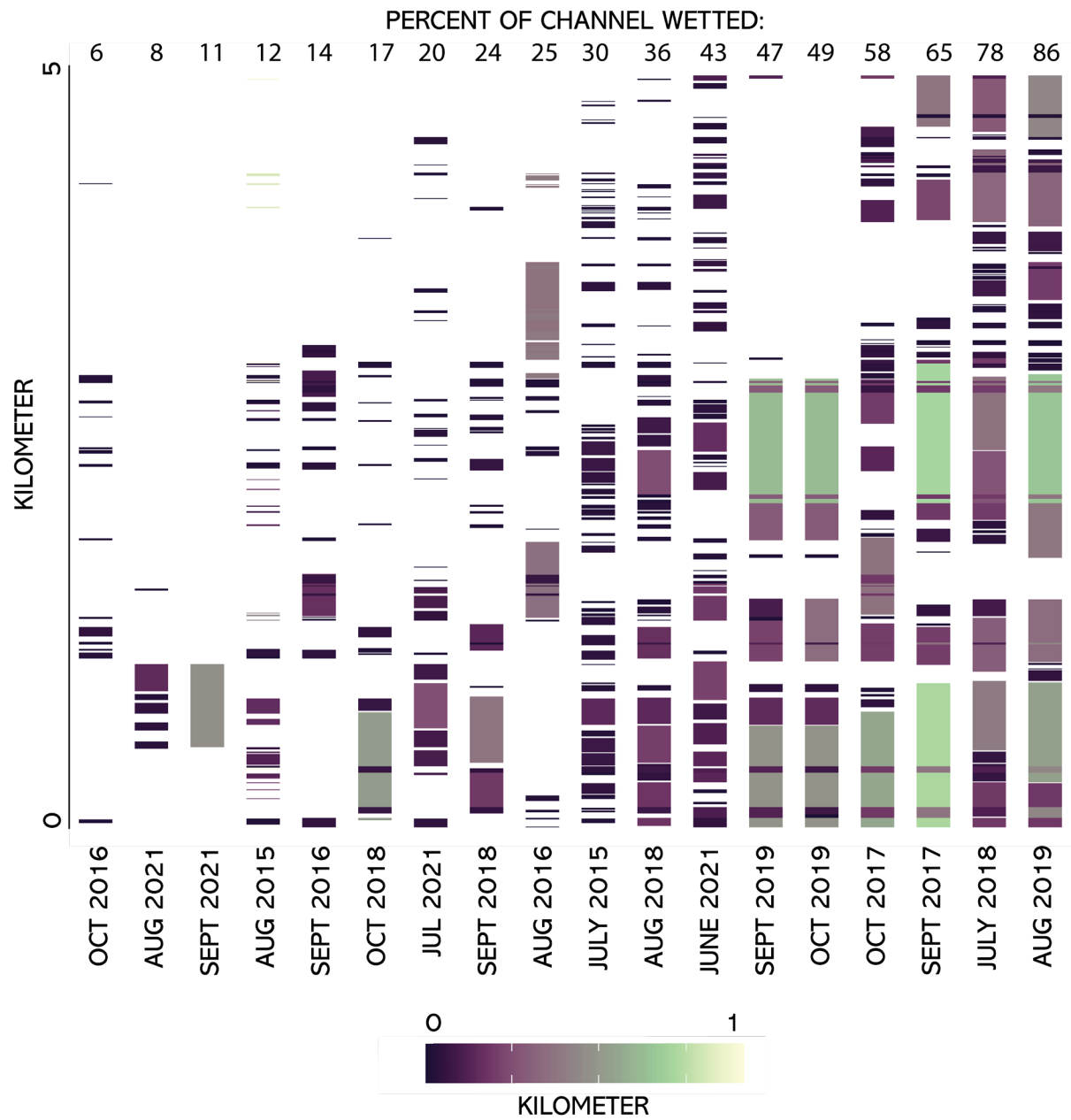
Figure S1. The spatial structure (distribution and length) of wet reaches along our study reach across time. Filled bars indicate a wet reach, with the color corresponding to the connected length of the wet reach. Thus, darker bars indicate shorter wetted lengths than lighter bars
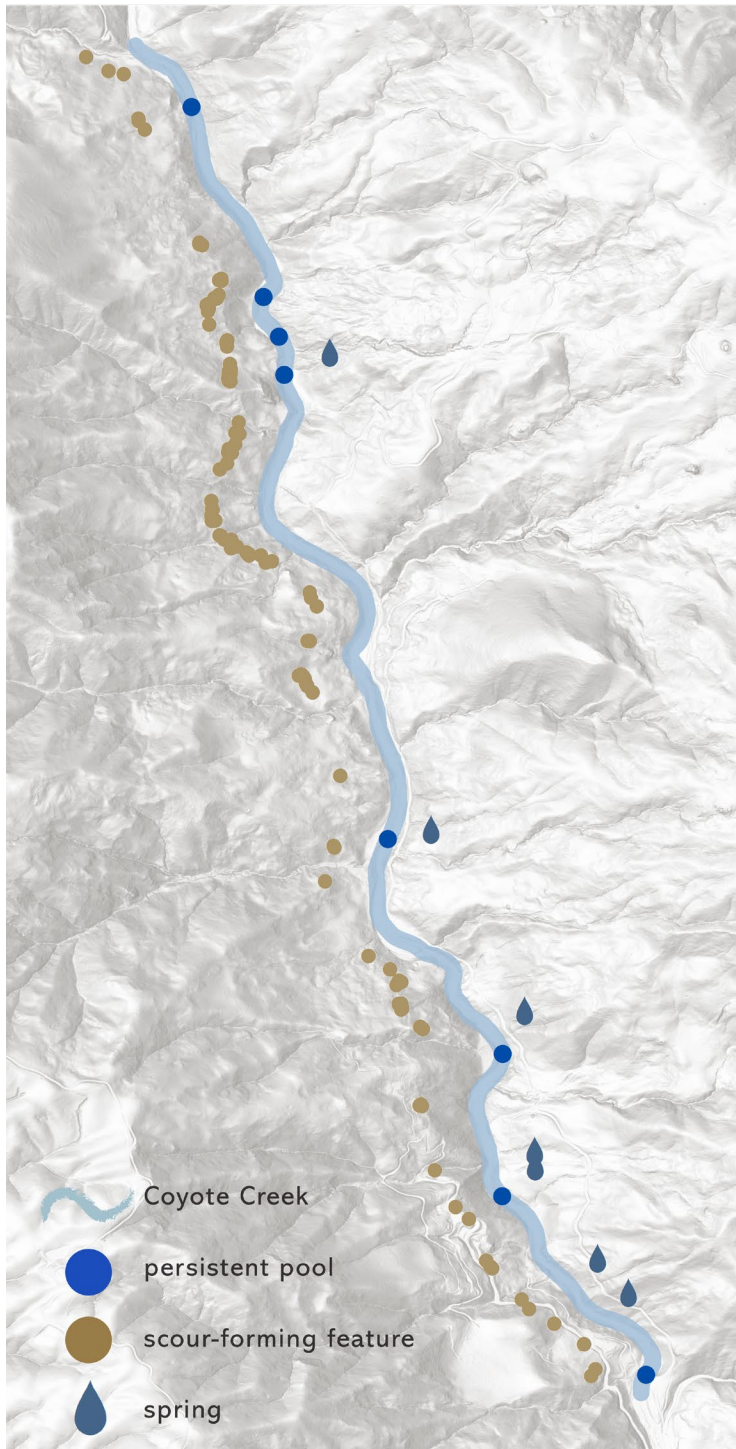
Figure S2. Location of permanent pools, scour-forming features such as boulders and exposed bedrock, and springs within our study reach. While 75% of permanent pools are associated with a scour-forming features, there are many locations of boulders and exposed bedrock that are not associated with permanent pools
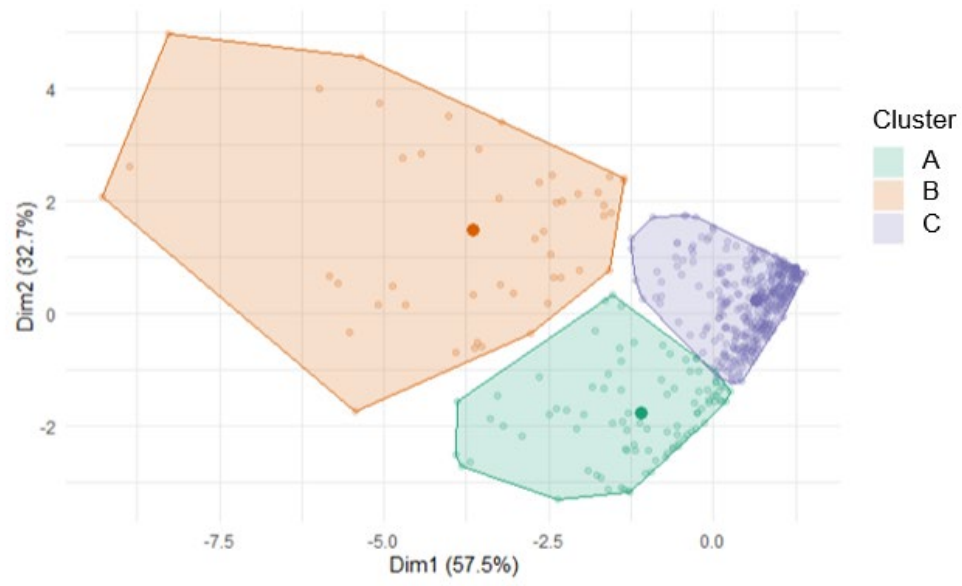
Figure S3. Results from the k-means clustering approach, yielding three distinct clusters.
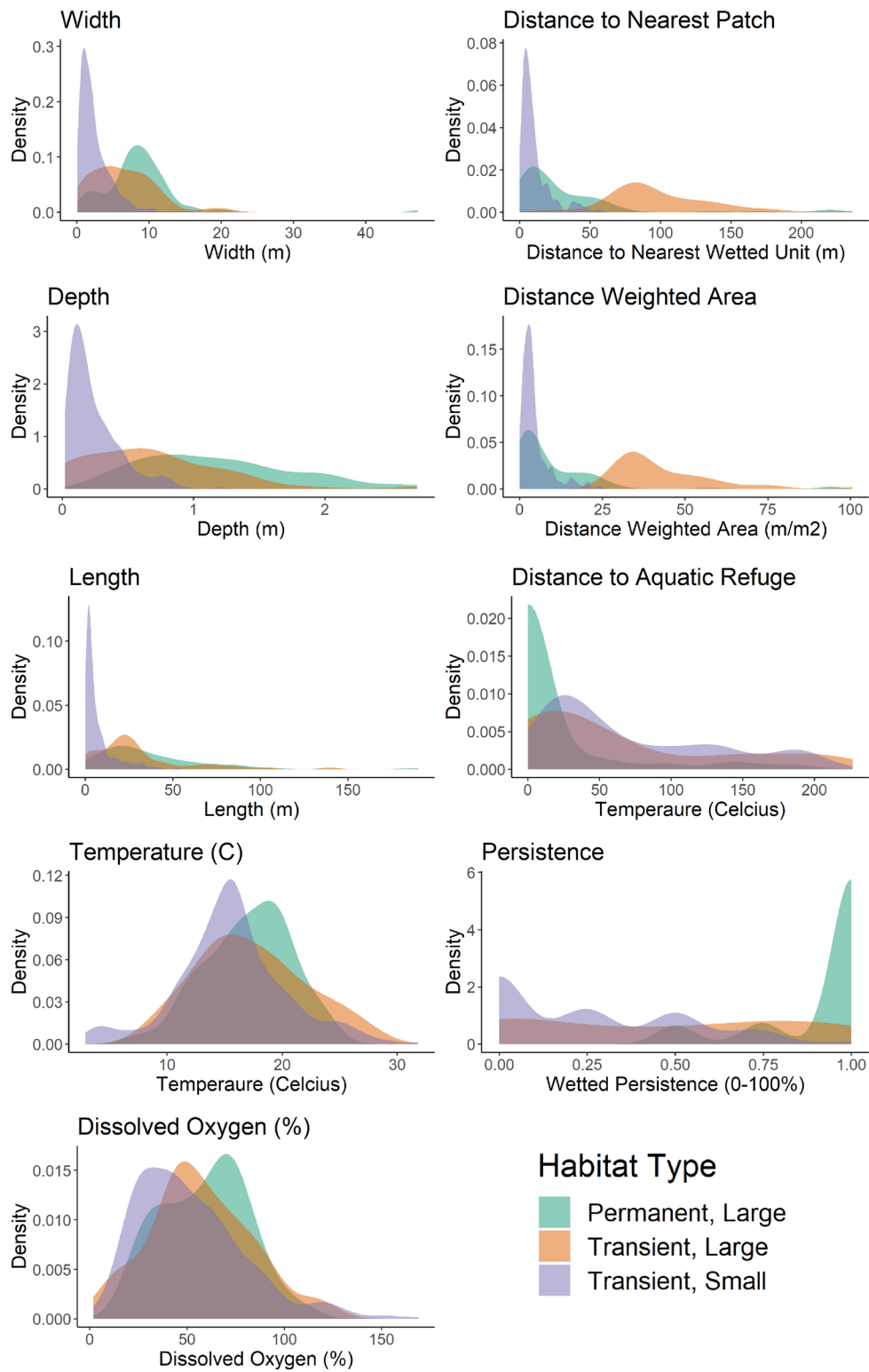
Figure S4. Distribution of predictor variables used in linear mixed models, separated by habitat type, using kernel density estimates.

Cluster	Ecological Characteristic	Wetted Persistence (0-100%)	Depth (m)	Distance to Nearest Wetted Habitat Unit (m)	Distance-Weighted Area (m/m²)
A	Persistent, large	91%	1.19	21.92	7.73
B	Transient, large	48%	0.77	108.26	45.37
C	Transient, small	26%	0.24	10.54	4.54

Table S2. Mean values of each variable used in the k-means clustering approach for each cluster.

CONCLUSION

In this dissertation, I explored the causes and consequences of interannual variability on wetted channel patterns. I showed that wetted channel dynamics are highly variable both within and across years, a characteristic that is impossible to capture using traditional monitoring methods. Using wetted channel surveys, I identified the various physiographic and climate factors that control the distribution and extent of intermittent conditions, and developed a modeling framework for predicting both the degree and variability of drying. I then evaluated how drying across space and time affects the distribution and abundance of species, by considering the wetted channel as a mosaic of shifting habitats. Given that the severity of intermittent stream conditions are expected to increase in coming years, particular attention must be given to these highly variable systems. Together, this work furthers our understanding of inter- and intra-annual intermittent stream dynamics, with strong applied implications, from monitoring to managing to conserving intermittent stream ecosystems.

As described in Chapter 1, widely used stream monitoring methods such as stationary gauges are largely inadequate in understanding the extent and variability of drying across the wetted channel in intermittent streams. Across all sites surveyed, few had a strong relationship between streamflow records and the wetted channel, and gauges were largely unable to capture wetted channel extent during zero- and low-flow conditions. For sites with congruent streamflow records and wetted channel extent, gauges were typically located in unaltered watersheds with minimal anthropogenic impacts. In other cases, gauges were useful in capturing locations of a priori interest, such as points of initial disconnection or habitat refuges. Such understanding can be applied to future hydrometric networks. We found that wetted channel mapping, a method that underpins much of this dissertation work, is accurate and effective, but is also resource intensive and limited in areas that are difficult to access or extensive in scale. However, this method has been shown to be possible through coordinated citizen science efforts, and further conservation and management efforts should consider developing community-based wetted channel survey initiatives. The work presented here has underscored the value of collecting a yearly snapshot of drying extent, and empowering citizens to engage with their watersheds by collecting such data can improve conservation action and help build a sense of stewardship more broadly. This may not be possible for all systems, and in those cases, alternative monitoring methods that are spatially and temporally explicit, such as deploying arrays of sensors or harnessing remote sensing technology, can be employed. Future monitoring of intermittent stream dynamics is required to understand how they may respond to altered climate conditions, and how this, in turn affects regional hydrological and ecological processes. Results from Chapter 1 emphasize the risks of using stationary tools in future monitoring campaigns.

In addition to monitoring, management approaches that incorporate the dynamism of wetted channels are required given an uncertain future. In Chapter 2, I identify the mechanisms that control wetted channel extent and variability, and used that understanding to develop predictive models more broadly. These models build in the non-stationarity of climate projections, and can

be applied to identify reaches of relative stability and concern, as well as determine areas that are vulnerable to increased intermittency. In this system and in many similar, emergency conservation interventions like fish rescues are often employed. These strategies are costly, labour-intensive, and time-sensitive, as it is difficult to predict when and where they will be needed. Using modelling frameworks such as described in this chapter, we can identify regions that may be buffered from climate fluctuations and can act as potential refuges that managers can work to maintain through in-stream or upland restoration strategies. Our work has also identified regions vulnerable to increased intermittency, which can be targeted for further monitoring and habitat recovery strategies, such as diversion curtailments during particularly dry years, or targeted flow releases to improve fish passage during key life history stages, such as spawning or outmigration. By knowing in advance which regions are disproportionately susceptible to drying, managers can work with landowners and water users to plan and adapt accordingly.

Chapter 3 underscores the value of monitoring wetted channel habitat to understand ecological dynamics across space and time. At Coyote Creek, though streamflow gauge readings consistently record zero-flow during the summer, wet-dry mapping surveys have identified a shifting mosaic of wetted habitat upstream. Despite extreme hydrologic variability, Coyote Creek continued to support native vertebrate species within and across years. The naturally intermittent conditions in our study reach prohibits the establishment of invasive species, while the perennial reaches downstream of storage reservoirs in the same system support more than a dozen nonnative fish species. Thus, drying is an important and beneficial phenomenon in these systems, and managers of historically intermittent systems that now have perennial flow due to anthropogenic alteration should consider reintroducing a period of flow cessation. Further, we found that our system exhibited remarkable resilience to intermittency and can overcome even extreme channel contraction via persistent refuge pools. Such pools acted as a 'keystone' habitat, harboring most of the species within the community and acting as an important source during rewetting. Conservation initiatives should work to ensure these habitats are maintained despite increasingly volatile climate conditions, either through in-stream restoration or supplementing water levels to increase refuge pool hydroperiod. Flow releases can also be used during particularly dry years to ensure the mosaic of intermittent habitats, including transient, small pools, are not lost. Such transient pools act as important habitat for specific species and life stages, including young-of-year fish. This system is at risk of losing important habitat supporting juvenile fishes under extreme climate conditions, with potential for recruitment failure and population collapse. Expanding this understanding to conservation initiatives can help prioritize resources adaptively depending on the water year.

Together, these three chapters underscore the need to monitor the spatial and temporal variability of drying in intermittent streams. This work has illuminated the patterns, controls, and consequences of such dynamism on the hydrology and ecology of intermittent stream environments, with clear connections for conservation and regulatory management. As disciplines working with intermittent streams continue to expand, inter- or intra-annual work should be prioritized. A moment in time is simply not enough to understand the processes that govern these systems. Further research into the response of specific species and life stages to

varying conditions, as well as the mechanistic connections between physical and climate variables on drying is needed. Intermittent streams have been long misunderstood compared to their perennial counterparts, suffering from inadequate and ever-changing legislative and regulatory protections. Growing recognition of their role in supporting critical environmental processes has inspired a body of work that will continue to support and advocate for intermittent stream appreciation and protection.

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