WETLAND HYDROLOGY AND GEOMORPHOLOGY

Hydrologic Connectivity and Flow Generation from California Vernal Pool, Swale, and Headwater Stream Complexes to Downstream Waters

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Abstract

Many headwater wetlands are integrated into flowpath networks and can serve as sources of streamflow for downgradient waters. We demonstrate this with five years of data in vernal pool, swale, and headwater stream complexes in the Central Valley, California. Long-term United States Geological Survey data suggest that the mean flow duration from the smallest watersheds in this region, including those with vernal pool, swale, and headwater stream complexes, is ~85 days per year. Our data concur, indicating that the annual days of flow per year from our vernal pool, swale, and headwater stream complexes ranges from ~20–200, but is ~85 when annual precipitation is 100% of normal. Peak stages are evident first in vernal pools which then propagate sequentially downstream through swales, headwater streams, and to the Sacramento River at celerities of ~1-1.5 m/s, consistent with expected flood wave velocities. Geospatial analyses show that these vernal pool, swale, and headwater stream features cover > 4% of the study area. Our results suggest these systems can be significant sources of streamflow, and therefore play an important role in maintaining the chemical, physical, and biological integrity of downstream waters, which has important implications for the definition of waters of the United States subject to regulation under the Clean Water Act.

Introduction

Hydrologic connectivity is the hydrologically mediated transfer of mass, energy, and/or organisms between landscape elements occurring by way of surface water and groundwater flowpaths (Pringle 2001, 2003). Hydrologic connectivity and hydrologic fluxes along flowpaths are controlled by climate, geology, and topography (Winter 2001). These fluxes occur at varying frequencies, magnitudes, timings, durations, and rates of change (Poff et al. 1997).

Integrated across the lateral, longitudinal, vertical, and temporal dimensions (Ward 1989), these flow characteristics comprise the natural flow regime (Poff et al. 1997), which in turn contributes to the chemical, physical, and biological integrity of receiving waters (Bonada and Resh 2013; Hershkovitz and Gasith 2013).

Wetlands occur in landscape positions where water tends to collect and are therefore embedded in flow networks (Neff et al. 2020). Within these flow networks, wetlands perform lag (i.e., detention), sink (i.e., retention), and source (i.e., transmission) functions (Rains et al. 2016), thereby cumulatively modulating downstream flow regimes (Cohen et al. 2016). However, while the functions of individual wetlands and their contributions to local-scale hydrology have been widely studied (e.g., Bullock and Acreman, 2003; Rains et al., 2006, 2008), the functions of wetland complexes and their cumulative contributions to watershed-scale hydrology have received less attention (Cohen et al. 2016; Rains et al. 2016; Lane et al. 2018). Additionally, though the role of headwater streams in maintaining the chemical, physical,

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and biological integrity of downstream waters is well established (Enviromental Protection Agency 2015; Creed et al. 2017), the role of individual headwater wetlands or interconnected complexes of headwater wetlands in maintaining the chemical, physical, and biological integrity of downstream waters is less well established (Enviromental Protection Agency 2015), and remains an area of active scientific inquiry (Cohen et al. 2016; Rains et al. 2016; Evenson et al. 2018b; Thorslund et al. 2018).

This needed inquiry is particularly critical for headwater wetlands that serve as the headward extent of flow networks (Enviromental Protection Agency 2015; Lane et al. 2018). Given the diffuse and distributed nature of upper catchments, headwater wetlands are numerous and comprise a large proportion of total wetland area in the United States (Lane and D'Amico 2016). They are commonly directly connected to or proximal to headwater streams, which comprise the majority of stream length in the United States (Nadeau and Rains 2007). Furthermore, and although there is accumulating evidence that they play important roles in maintaining the chemical, physical, and biological integrity of downstream waters (Evenson et al. 2018a; Thorslund et al. 2018), general rules about if, how, and the degrees to which they do so remain lacking (Enviromental Protection Agency 2015; Lane et al. 2018). Additionally, these features are difficult to identify, catalog, and map due to their small size, abundance, and density (Meyer et al. 2007; Lang et al. 2012; Lane and D'Amico 2016), as well as tendency towards seasonal or intermittent flow, making them particularly vulnerable to loss (Van Meter and Basu 2015; Creed et al. 2017).

Vernal pools are wetlands that occur in low-elevation headwater settings in southern Oregon, California, northern Baja California, and other Mediterranean climates of the world (Stebbins 1976; Riefner and Pryor 1996). They are associated with specific types of geological formations, landforms, and soils (Hobson and Dahlgren 1998; Smith and Verrill 1998), and therefore tend to be clustered at the landscape scale. These clusters of vernal pools commonly occur on high terrace features, and which we hereafter call vernal pool landscapes. These vernal pool landscapes are particularly prominent in the Central Valley of California, where they cover more than 4100 km^2, or ~ 5%, of the total land surface (Holland 1996, 1998). Here, they commonly form the headward extent of small watersheds that drain the valley bottom to the Sacramento River in the north and the San Joaquin River in the south (Smith and Verrill 1998).

On these vernal pool landscapes, vernal pools, swales, and headwater streams commonly occur in integrated complexes. These vernal pool, swale, and headwater stream complexes are coupled surface water and shallow perched groundwater systems with strongly seasonal hydrographs, being drained and dried in the pronounced dry season, and inundated and connected to one another and to downstream waters during the equally pronounced wet season (Rains et al. 2006, 2008). In this way they may serve as part of the variable source area as they connect hydrologically to each other and communicate water to downgradient waters (Dunne and Black 1970; Hewlett and Nutter 1970). Although a great deal is known about the hydrology of these vernal pools, swales, and headwater streams at the local scale (e.g., Hanes and Stromberg, 1998; Rains et al., 2006, 2008), far less is known about if and to what extent they support hydrologic functions at the landscape or watershed scales (e.g., Cohen et al., 2016). This understanding is especially needed because these vernal pool landscapes are rapidly undergoing transformation from passive land uses such as grazing to more active land uses such as irrigated agriculture, including for walnuts and almonds (e.g., Tehama County Department of Agriculture, 2021), and are being lost at high rates (Holland 1996, 1998).

This work aims to expand understanding of hydrologic connectivity in headwater wetland settings. In this study, we use these vernal pool, swale, and headwater stream complexes as model systems to study whether and the extent to which headwater wetlands contribute to the maintenance of the physical integrity of downstream waters. We show that vernal pool, swale, and headwater stream complexes are prevalent, especially in headwater positions. We show that these features act as part of the variable source area, hydrologically connecting to each other and to downstream waters. Once hydrologically connected, we demonstrate that vernal pool, swale, and headwater stream complexes serve as sources of streamflow, thereby making substantial contributions to the physical integrity of downstream waters.

Methods

Study Area

Our study focused on the Coyote Creek and Oat Creek watersheds (157 km^2) located on the west side of the northern Central Valley, California, USA (Fig. 1). Coyote Creek drains to Oat Creek, Oat Creek drains to the Sacramento River, and the Sacramento River drains thereafter to the Sacramento-San Joaquin River Delta, San Francisco Bay, and finally the Pacific Ocean. Both are in Tehama County, which has one of the highest densities of vernal pools in the Central Valley (Holland 1996, 1998).

The study area climate is Mediterranean, characterized by mild, wet winters and hot, dry summers (Red Bluff Municipal Airport, Station 24,216, 1981–2010). The mean, maximum, and minimum daily temperatures are 17.1 °C,
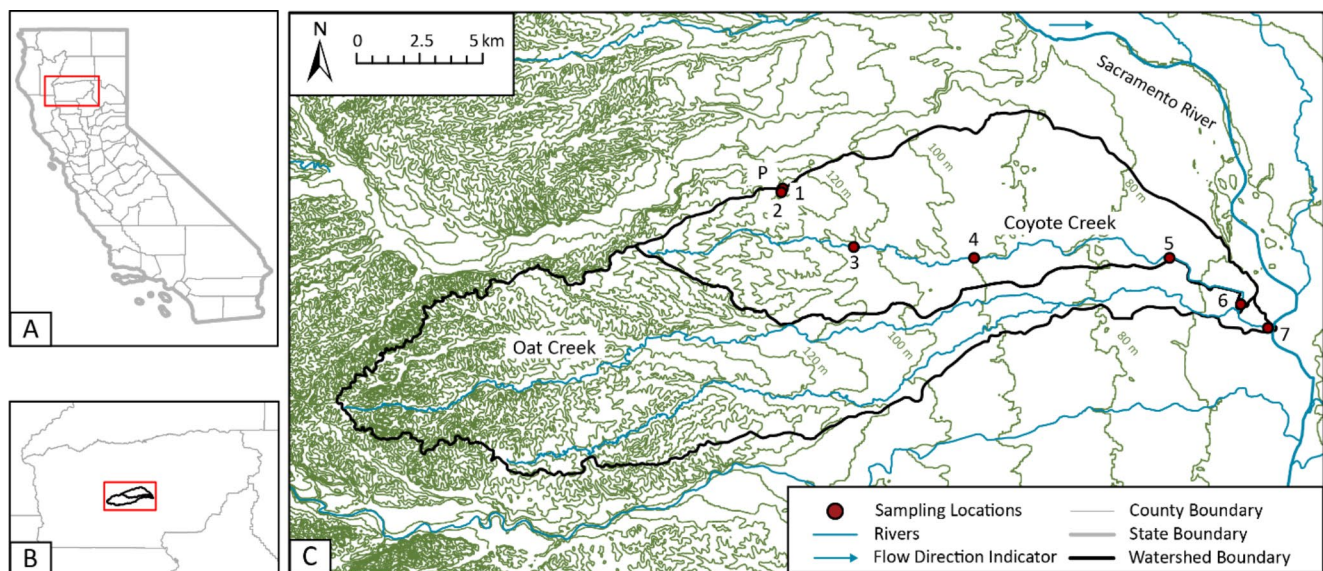
Fig. 1 Study area location, and location of precipitation (P) and water level gages (1–7) in the study area. **A**: Location of Tehama County in the northern Central Valley of California, U.S.A. **B**: Location of study area within Tehama County, California. **C**: Coyote Creek and Oat Creek watersheds west of the Sacramento River

23.9 °C, and 10.2 °C, respectively. Mean annual precipitation is 62.20 cm. Intra-annual variability is high, with a pronounced dry season during which ~ 5% of the annual precipitation falls (June-September) and a pronounced wet season with intermittent periods of low-intensity and short periods of high-intensity precipitation during which ~ 95% of the annual precipitation falls (October-May). Interannual variability also is high, even in comparison to other Mediterranean climatic regions worldwide (Bonada and Resh 2013), with total annual precipitation being as low as 35.1 cm (water year 2008) and as high as 116.6 cm (water year 1995).

Both east and west sides of the Sacramento Valley are draped with Pleistocene to Pliocene alluvial fans terminating at the Holocene basin floor along the Sacramento River (Jennings et al. 2010). These alluvial fans are nearly level to undulating but gently slope toward the basin floor. They have well-developed drainage networks, being dissected by streams and rivers that are tributaries of the Sacramento River. Major geologic formations include the Red Bluff formation on the high terraces and the Riverbank formation on the low terraces and floodplains, though other similarly situated and developed formations occur. The Red Bluff formation comprises a thin veneer of highly weathered, bright-red gravels, sands, and silts overlying terrace and fan deposits of the Laguna, Tehama, and Tuscan formations, and is 450 K-1.08 M BP in age, while the Riverbank formation is characterized by weathered reddish gravel, sand, and silt forming terraces and fans, and is 130-450 K BP in age (Helley and Harwood 1985). Both the Red Bluff and Riverbank geologic formations are old enough for substantive

soil-forming (i.e., pedogenic) processes to have occurred (Helley and Harwood 1985; Smith and Verrill 1998). The different formations and ages are reflected in different soil types (Soil Survey Staff - NRCS/USDA, 2019). On the high terraces, the dominant NRCS soil map units are the Corning, Redding, and Corning-Redding complex. On the low terraces, the dominant NRCS map unit is the Arbuckle series, including the "clayey substratum" and the "clayey substratum channelized" phases, though Riverwash map units are included along the larger streams. Inclusions of hydric soils are common in all of these soil types, consistent with the presence of numerous vernal pool, swale, and headwater streams complexes.

Vernal pool landscapes occur on both the Red Bluff and Riverbank formations, but most especially on the Red Bluff formation with the Corning, Redding, and Corning-Redding complex soils. Though these landforms slope gently toward the basin floor, fine-scale microtopography is pronounced. The primary microtopography consists of hummocks and hollows that occur as series of raised areas (i.e., hummocks) and interconnected vernal pools and swales (i.e., hollows). Drainage patterns are typically deranged, with some vernal pools draining in more than one direction. Where drainage basins are large enough and slopes are steep enough, swales transition into headwater streams with continuous bed and bank features and intermittent flows. These headwater streams occur most often along the high terrace scarps and flow into larger streams, including Coyote Creek, Oat Creek, and thereafter the Sacramento River.

Land use-land cover is typical of the Mediterranean California ecoregion, and include grasslands, open oak

woodlands, mixed agriculture, and low density development (Commission for Environmental Cooperation, 1997; Klausmeyer and Shaw, 2009; Underwood et al., 2009; Cox and Underwood, 2011). In the headwater settings, agriculture is predominantly dryland grazing. On the lower reaches of Coyote Creek and Oat Creek, agriculture is predominantly irrigated walnut and olive orchards. Much of the headwater settings are designated critical habitat for the U.S. federally listed (threatened) vernal pool fairy shrimp (*Branchinecta lynchi*). The lower reaches of Coyote Creek and Oat Creek are designated critical habitat for the U.S. federally listed (threatened) Central Valley spring-run Chinook salmon (*Oncorhynchus tshawytscha*) and Central Valley steelhead (*Oncorhynchus kisutch*). These salmonids use lower reaches of Coyote Creek and Oat Creek as spawning and rearing habitat and are therefore particularly sensitive to perturbations in streamflow and stream temperature (Katz et al. 2013; Lorig et al. 2013).

Mapping of Vernal Pool Landscapes and Features

We mapped vernal pool landscapes and the frequency of vernal pools, swales, and headwater stream features on those vernal pool landscapes in both the Coyote Creek and Oat Creek watersheds using a combination of field work and geospatial analyses.

We first mapped all vernal pool landscapes in both the Coyote Creek and Oat Creek watersheds in ArcGIS Pro 2.8.3 (ESRI, Redlands, California). We began by delineating watershed boundaries as per the National Hydrography Dataset, or NHD (United States Geological Survey, 2019). We then identified all high terraces where the Red Bluff formation occurred using topographic maps and geologic maps and reports (Helley and Harwood 1985; Jennings et al. 2010) and where the Corning, Redding, and Corning-Redding complex soils occurred using a web-based soil survey database (Soil Survey Staff - NRCS/USDA, 2019). We then examined aerial imagery to identify regions exhibiting the pronounced dimpled hummock and hollow microtopography characteristic of these vernal pool landscapes (ESRI, 2022). We cross-validated the extent of this mapping by comparing our results to previously published inventories of vernal pool landscapes (Holland 1996, 1998; United States Fish and Wildlife Service, 2020).

We conducted a frequency analysis to determine the prevalence of vernal pool, swale, and headwater stream features on mapped vernal pool landscapes in two representative parcels in the Coyote Creek watershed (Fig. 2). One was a 225-ha parcel on the Coyote Creek Conservation Area (hereafter called the west parcel), which is managed for ecological conservation. The other is a 282-ha parcel adjacent to the Coyote Creek Conservation Area (hereafter called the

east parcel), which was in similar condition to the Coyote Creek Conservation Area prior to land preparation activities in late 2012, which included ripping, slip plowing, scraping and filling (i.e., land leveling), road construction, and other earthwork activities. Prior to conducting the frequency analyses, we field trained at 33 locations (4 on the west parcel and 29 on the east parcel), documenting vegetation, soil, and hydrology conditions on Wetland Determination Data Forms—Arid West Region (US Army Corps of Engineers, 2015). On the east parcel, we used procedures for non-Normal Circumstances due to the land preparation activities in late 2012 (U.S. Army Corps of Engineers - Environmental Laboratory, 1987).

We conducted the frequency analysis using ArcGIS 10.2 (ESRI, Redlands, California). We created a grid overlay with 6 m spacing across each parcel, which resulted in 60,536 locations (nodes) on the west parcel and 75,879 nodes on the east parcel. We then randomly selected 1% of the nodes on each parcel to be part of the frequency analysis dataset, resulting in 1,365 frequency nodes (i.e., 606 on the west parcel, 759 on the east parcel). We determined whether each frequency node occurred in a wetland feature (i.e., a vernal pool, swale, or headwater stream) or in a nonwetland feature (i.e., an upland) by viewing imagery (true color and infrared) and reference datasets including the NHD, National Wetlands Inventory (NWI), ArcGIS USA_Topo layer, and ArcGIS World_TopoMap. There were two reference imagery sources: GeoEye1 (May 1, 2010) and, secondarily, Pleiades (June 18, 2014). Both were obtained from LandInfo, Inc. as 4-band pan-sharpened orthorectified GeoTIFF files and were viewed at scales of up to 1:200. As validation, we randomly selected 94 of the previously classified nodes for reclassification by another observer.

Microtopography and Soils

We assessed potential surface water storage in vernal pool landscapes by characterizing microtopography at randomly selected representative locations. We surveyed microtopographic variation along four 90-m cross-sections using a Topcon AT-B Series Automatic Level (Topcon Positioning Systems, Inc., Livermore, CA) or a Spectre Precision Laser GL 412 Laser Level System (Spectra Precision, Westminster, CO). All four transects were located on parcels managed for ecological conservation, including two within the Coyote Creek Conservation Area and two within the Thomes Creek Ecological Reserve. The Thomes Creek Ecological Reserve is located in the McClure Creek watershed, south of the Coyote Creek and Oat Creek watersheds. The Thomes Creek Ecological Reserve was used because it is the only other nearby publicly accessible and intact vernal pool landscape in the immediately surrounding physiographic
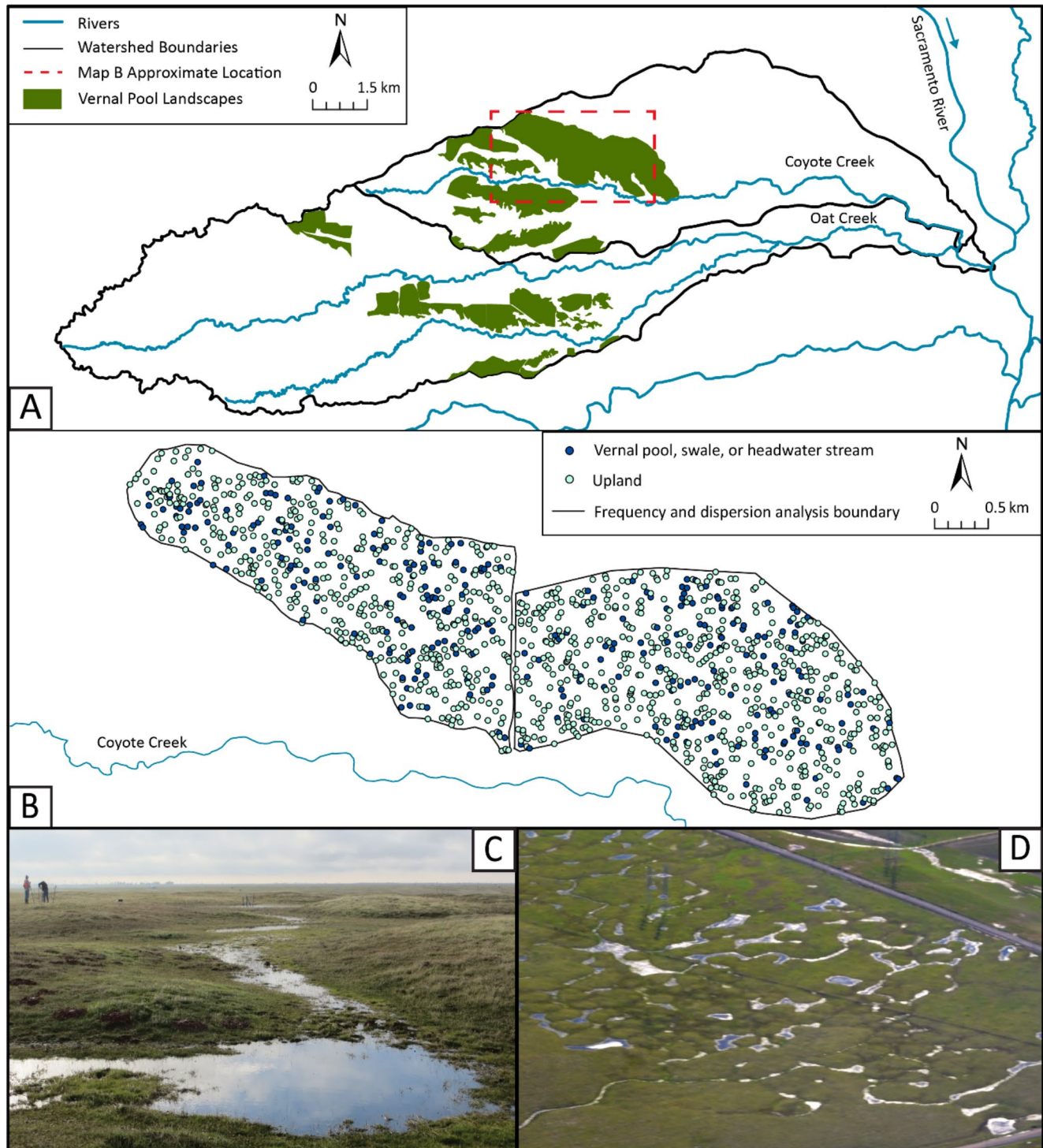
Fig. 2 Locations of delineated vernal pool landscapes in the Coyote Creek and Oat Creek watersheds, locations of points classified in the frequency analysis on two representative parcels in the Coyote Creek watershed, and photographs showing characteristic vernal pool landscapes. **A**: Distribution of vernal pool landscapes in the Coyote Creek and Oat Creek watersheds. **B**: The spatial distribution of random classification points on the two representative parcels in the Coyote Creek watershed used in the frequency analysis. Points were classified as wetland features (i.e., area inside a vernal pool, swale, or headwater stream feature) or non-wetland features (i.e., areas outside a vernal pool, swale, or headwater stream feature). **C and D**: A ground-level view (**C**) and aerial view (**D**) of vernal pool landscapes containing vernal pools, swales, and headwater streams in the study area

region of the study area. We characterized general land-surface slope with least-squares regression, with relative elevation as the dependent variable and relative distance along the transect as the independent variable. We then characterized microtopographic relief along that general land-surface slope by taking the mean ± SD absolute value of the residuals of that least-squares regression, i.e., the mean ± SD of the relative elevation deviations above and below that general land-surface slope.

We assessed potential shallow groundwater storage in vernal pool landscapes by characterizing soils at representative locations. We first obtained soils data from the USDA Natural Resources Conservation Service Web Soil Survey (Soil Survey Staff - NRCS/USDA, 2019). We then field characterized soils at 33 locations, 4 on the west parcel on the Coyote Creek Conservation Area and 29 on the east parcel adjacent to the Coyote Creek Conservation Area. We dug soil pits to depths of 1–2 m with a Takeuchi TB180 Crawler Excavator (Takeuchi Manufacturing, Sakaki, Nagano, Japan) and described soil profiles consistent with guidance in the U.S. Department of Agriculture Soil Survey Manual (Soil Science Staff, 2017).

Physical Hydrology

We characterized physical hydrology using a combination of publicly available data and our own field data. We first used U.S. Geological Survey (USGS) streamflow data to determine the relationship between watershed area and the mean annual days of streamflow in this physiographic region, using this relationship to infer the annual days of flow expected from the smallest watersheds, including vernal pool, swale, and headwater stream complexes. We then used precipitation and stage data to determine when and for what duration vernal pools, swales, and headwater stream complexes serve as sources of streamflow to downstream waters.

Runoff generation and resulting streamflow are controlled by interactions between climate, geology, and topography, and therefore tend to be similar within a given physiographic setting (Winter 2001). We used USGS data to determine the relationship between watershed area and mean annual days of flow (i.e., $Q > 0$) on other intermittent streams in the same physiographic setting as the Coyote Creek and Oat Creek watersheds (i.e., watersheds that drained the foothill, toeslope, and valley bottom settings on the west side of the northern Central Valley). We selected only those streams with at least three years of daily flow data. This resulted in seven streams, with mean ± SD period of record being 16 ± 8 years.

We acquired hourly precipitation data from two publicly available sources, the National Oceanic and Atmospheric Administration (NOAA), Red Bluff Station 24,216 and the California Department of Water Resources, California Irrigation Management System (CIMIS), Stations Gerber Station 8/Gerber South Station 12 (Gerber Station 8 was replaced by Gerber South Station 12 at the end of water year 2014). We also collected event-based precipitation data using a "tipping-bucket" rain gage located in the headwaters of the Coyote Creek watershed (Onset Corporation, Bourne, MA). The frequency, magnitude, timing, and duration of precipitation measured at these stations were consistent. We therefore used the hourly precipitation data from the NOAA Red Bluff Station 24,216 and assumed those data were indicative of precipitation throughout the watershed.

We collected sub-hourly water level data for water years 2013–2017 at seven locations sequentially downgradient along a stream network, beginning in a vernal pool, through its draining swales, headwater streams, Coyote Creek and Oat Creek, and ending just above the confluence of Oat Creek with the Sacramento River (Fig. 1; Table 1). Shallow monitoring wells/stage gages were constructed from 5 cm inside diameter PVC standpipe with 0.010 slots to the surface. We recorded water levels inside the shallow monitoring wells/stage gages using pressure transducers and data loggers (Onset Corporation, Bourne, MA).

We used the precipitation and stage data to conduct storm peak translation and pressure head propagation rate analyses

Table 1 Site identifications, names, elevations, and river kilometer measurements of precipitation and water level gages in the study area (Fig. 1). One precipitation gage (P) was placed adjacent to the vernal pool (Location 1). Seven water level gages were placed along the Coyote Creek stream network, beginning in the vernal pool, its draining swale, and subsequently downgradient locations culminating with the confluence of Oat Creek with the Sacramento River

Site ID	Feature Name	Elevation (m above sea level)	River kilometer
P	Precipitation Gage	134	0
Location 1	Vernal Pool	134	0
Location 2	Swale	134	0.045
Location 3	Coyote Creek at Paskenta Rd.	103	1.61
Location 4	Coyote Creek at Corning Canal	89	3.50
Location 5	Coyote Creek at Tehama Colusa Canal	72	6.37
Location 6	Coyote Creek at Sacramento Wildlife Refuge	68	7.75
Location 7	Oat Creek at Sacramento River	65	8.29

using the MathWorks computer program MATLAB version 9.4. We analyzed data from nine storm events between October 2012-August 2016 to demonstrate flow generation from a vernal pool landscape and subsequent flow propagation through the watershed to the Sacramento River. These storm events were selected because they were identifiable as discrete storm events followed by a flood wave during a time when continuous data were available for all seven gage locations.

Results

Mapping of Vernal Pool Landscapes and Features

Vernal pool landscapes are prevalent in both the Coyote Creek and Oat Creek watersheds (Fig. 2A). They are more prevalent in the Coyote Creek watershed, where they comprise 20% of the land surface, and comparatively less prevalent in the Oat Creek watershed, where they comprise 8% of the land surface. Overall, they comprise 13% of the total land surface of the combined watersheds.

Vernal pool, swale, and headwater stream features are prevalent in these vernal pool landscapes (Fig. 2B). On the west parcel, 23% (141 of 606) of the randomly selected frequency nodes were located in a vernal pool, swale, or headwater stream, and 77% (465 of 606) were located in non-wetland features (i.e., uplands). On the east parcel, 18% (136 of 759) of the randomly selected frequency nodes were located in a vernal pool, swale, or headwater stream, and 82% (623 of 759) were located in non-wetland features. These data indicate that vernal pool, swale, and headwater stream features cover 20% of these vernal pool landscapes. These results were validated by the independent reclassification of 94 locations. Results of this validation are tabulated in a confusion matrix (Table 2). The overall accuracy (i.e., the total number of agreements/total number of attempts) is 81/94, or 86%.

Combining these results, vernal pool, swale, and headwater stream features comprise at least 4.0% of the Coyote Creek watershed and 1.6% of the Oat Creek watershed, or 2.6% of the combined watersheds. These estimates do not include vernal pool, swale, and headwater stream complexes that occur in lower densities on other landforms,

such as the Riverbank soil formation on the low terraces and floodplains in Coyote Creek and Oat Creek watersheds.

Microtopography and Soils

Microtopography on the representative sites is typical of vernal pool landscapes (Fig. 3). The overall land surface is nearly level, with slopes of ≤1%. Local microtopographic variation is small but frequent. Mean ± SD absolute values of the residuals around detrended mean elevations range from a high of 0.22 ± 0.1 m (Fig. 3A) to a low of 0.14 ± 0.10 m (Fig. 3C). Local low elevation sites are typically vernal pools, swales, and headwater streams, which is consistent with both their small cross-sectional areas and their close proximity to one another.

Soils on the representative sites are also typical of vernal pool landscapes (Hobson and Dahlgren 1998; Smith and Verrill 1998) (Fig. 4). The modal soil is the Corning-Redding complex, though Corning and Redding soils also are prevalent. Corning soils consist of very deep, well, or moderately well drained soils formed in gravelly alluvium weathered from mixed rock sources. Redding soils consist of well or moderately well drained soils formed in alluvium derived from mixed sources. Both are commonly associated with hummock and hollow microtopography, and both are on the national and Tehama County hydric soils lists due to unnamed hydric inclusions found in the microtopographic lows (i.e., the vernal pools, swales, and headwater streams). Riverwash occurs in a few locations in some large swales and well-defined streams. Riverwash generally consists of stratified gravelly sand to extremely gravelly coarse sand within drainage ways. Riverwash also is on both the national and Tehama County hydric soils lists. Field observations confirm the presence of all of these soils, including the presence of the hydric soil inclusions in the Corning and Redding soils.

Both Corning and Redding soils have Bt horizons, which are accumulations of silicate clay formed in the horizon and/or moved into the horizon by illuviation. Though individually thin (e.g., <20 cm), there are commonly multiple Bt horizons within the upper 1 m of soil profiles. These horizons are firm, sticky, plastic, and clay-rich, and therefore are slowly permeable. Redding soils also have Bsm and/or Bqm horizons, which are continuous or nearly continuous

Table 2 Confusion matrix generated from the vernal pool, swale, and headwater stream complex frequency analysis accuracy assessment (Fig. 2). The frequency analysis classified points as wetland features (i.e., area inside a vernal pool, swale, or headwater stream feature) or non-wetland features (i.e. areas outside a vernal pool, swale, or headwater stream feature). Classification was first performed by the primary mapper (K. Rains) on 1,365 frequency nodes. Reclassification was then performed by the validation mapper (Stepchinski) on 94 of these 1,365 frequency nodes

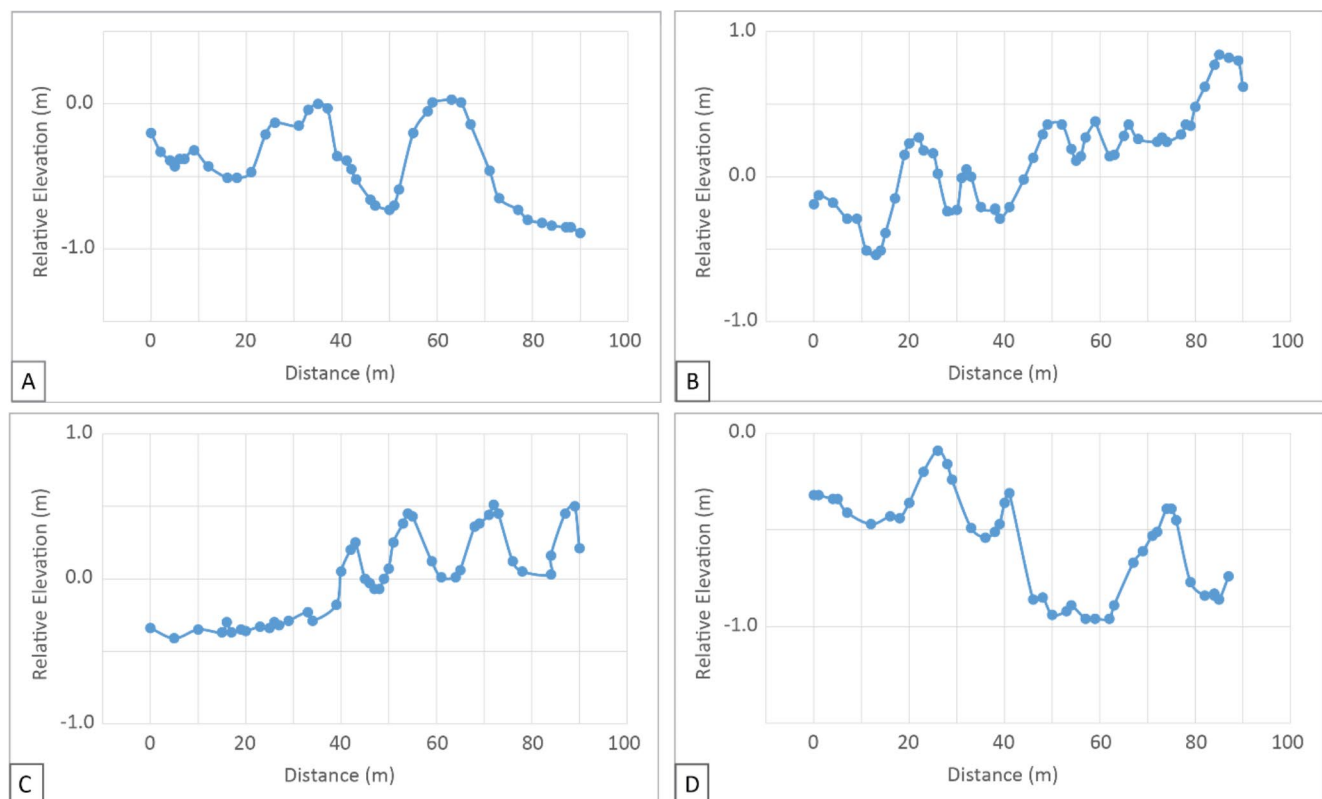|		Original Classification	
		Wetland Feature	Non-Wetland Feature
Reclassification	Wetland Feature	16	9
	Non-Wetland Feature	4	65

Fig. 3 Microtopographic variation in four vernal pool, swale, and headwater stream complexes. **A**: Elevations recorded along a transect at the Coyote Creek Conservation Area, where slope is 0.4% and mean ± SD absolute value of the residuals around the detrended mean elevation is 0.22 ± 0.13 m. **B**: Elevations recorded along a transect at the Coyote Creek Conservation Area, where slope is 1% and mean ± SD absolute value of the residuals around the detrended mean elevation is 0.16 ± 0.10 m. **C**: Elevations recorded along a transect at the Thomes Creek Ecological Reserve, where slope is 1% and mean ± SD absolute value of the residuals around the detrended mean elevation is 0.14 ± 0.10 m. **D**: Elevations recorded along a transect at the Thomes Creek Ecological Reserve, where slope is 0.5% and mean ± SD absolute value of the residuals around the detrended mean elevation is 0.15 ± 0.13 m

iron- or silica-cemented duripans. These are thick (e.g., > 20 cm) and commonly within the upper 1–2 m of the soil profile. These horizons are massive, indurated with iron and/or silica, and only slightly fractured, and therefore are also slowly permeable. Again, field observations confirm the presence of these slowly permeable horizons.

Physical Hydrology

The seven USGS stream gages used for this study were on streams with watershed areas ranging from 98.9 to 562 km^2 and had mean annual days of flow ranging from 106 to 317 days (Table 3). Mean annual days of flow is a strong linear function of watershed area, with $R^2 = 0.97$ and $p < 0.01$ (Fig. 5). If the trend line of this relationship is extended back to the origin, then the duration of flow from the smallest watersheds would be ~ 85 days. This suggests that the vernal pool, swale, and headwater stream complexes could be expected to have ~ 85 days of flow in a normal year.

Over five years, total annual precipitation ranged from 370 to 706 mm, or 59–114% of normal (Table 4). Over that same interval, the duration of inundation in the vernal pool (Location 1, Fig. 1) ranged from 63 to 172 days, and the duration of flow from the vernal pool, swale, and headwater stream complex (Location 2, Fig. 1) ranged from 19 to 110 days (Table 4). The duration of inundation in the vernal pool and duration of flow from the vernal pool, swale, and headwater stream complex are strong linear functions of percent normal precipitation (Fig. 5). Duration of inundation in the vernal pool had an $R^2 = 0.69$ and $p < 0.10$, and duration of flow from the vernal pool, swale, and headwater stream complex had an $R^2 = 0.93$ and < 0.01. Projecting to 100% of normal precipitation, this also suggests that the vernal pool, swale, and headwater stream complex could be expected to have ~ 85 days of flow in a normal year.

We analyzed precipitation and stages from seven stage gages located sequentially downgradient to determine whether peak flows could be traced as they are translated from the vernal pool, its draining swale, headwater streams, Coyote Creek and Oat Creek, and ending just above the confluence of Oat Creek with the Sacramento River (Fig. 1). Each of the nine peak flows (Fig. 6) selected initiated first in
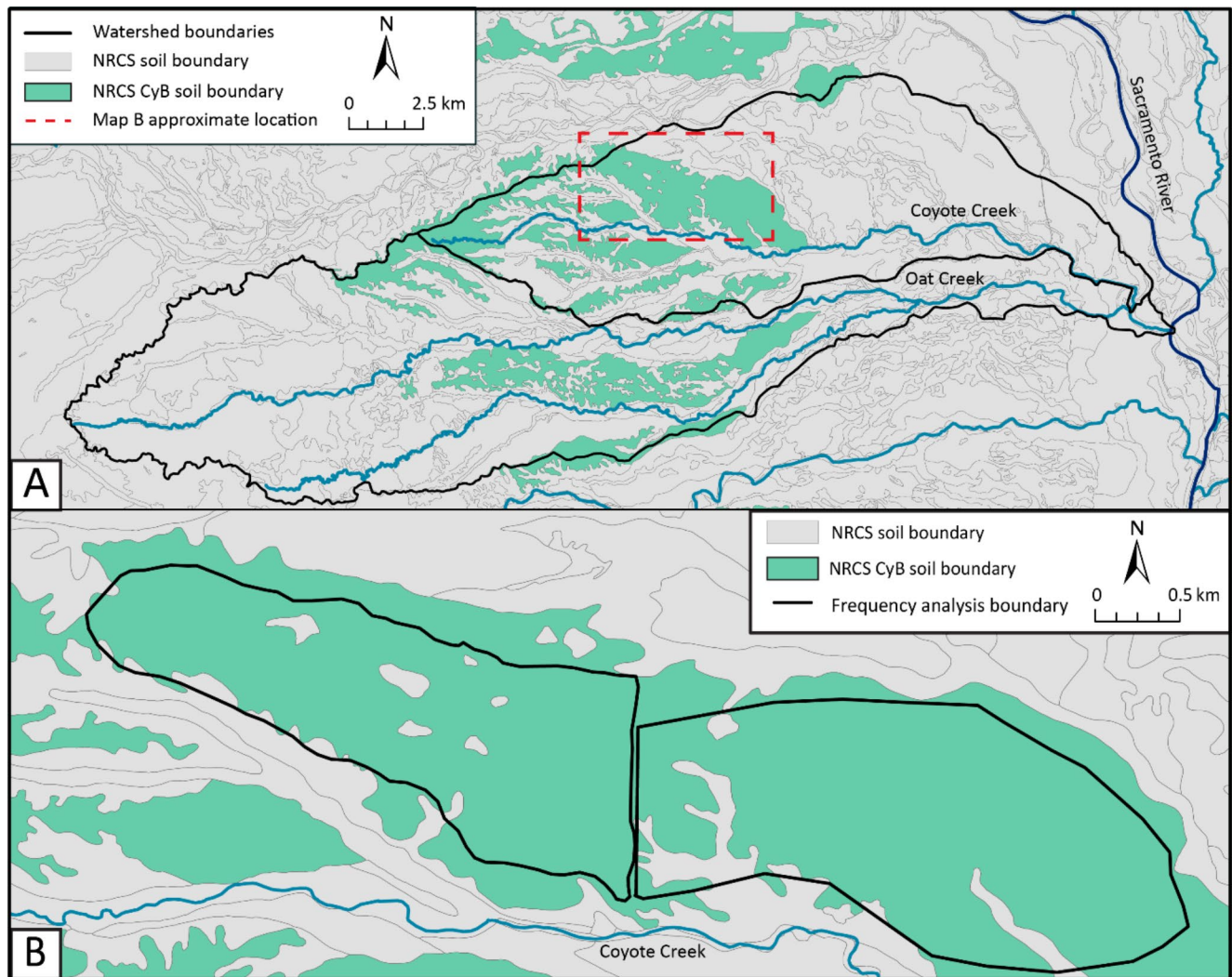
Fig. 4 Spatial distribution of a modal soil series, Corning-Redding Complex (CyB), supporting vernal pool landscapes **A**: in the Coyote Creek and Oat Creek watersheds and **B**: on the two representative par- cels (i.e., the west and east parcels) in the Coyote Creek watershed utilized in the frequency analysis (Soil Survey Staff - NRCS/USDA, 2019)

Table 3 USGS stream gages used to characterize the relationship between watershed area and mean annual days of flow in seven other watersheds in this physiographic region (Fig. 5A).

Stream Gage ID	Period of Record (Water Years)	Total Years of Record	Water-shed Area (km²)	Mean Annual Days of Flow (i.e., Q > 0)
USGS 11,390,672 [1]	1959–1985	27	98.9	142
USGS 11,390,655 [2]	1964–1978	15	100.8	106
USGS 11,378,800 [3]	1960–1982	23	242.2	186
USGS 11,378,860 [4]	1965–1967	3	282.3	209
USGS 11,380,000 [5]	1931–1941	11	336.7	233
USGS 11,380,500 [6]	1950–1969	20	352.2	243
USGS 11,375,820 [7]	1963–1978	16	562.0	317

Locations: [1] Stone Corral Creek near Sites, CA [2] South Fork Willow Creek near Fruto, CA [3] Red Bank Creek near Red Bluff, CA [4] Red Bank Creek at Rawson Road near Red Bluff, CA [5] Elder Creek near Henleyville, CA [6] Elder Creek at Gerber, CA [7] South Fork Cottonwood Creek near Cottonwood, CA
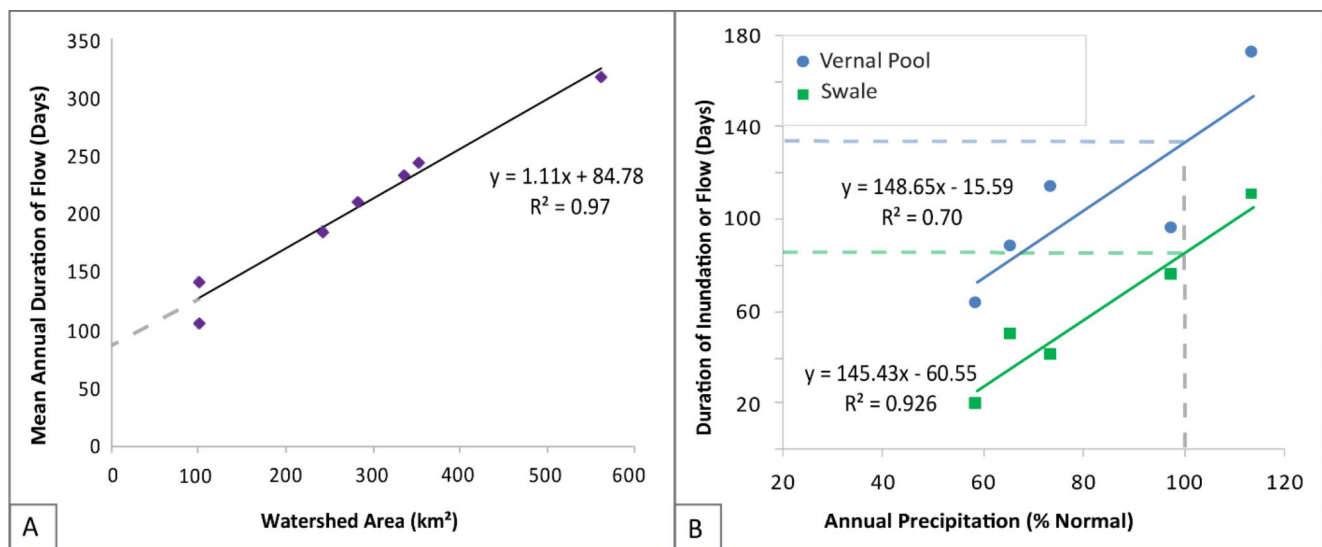
Fig. 5 The relationship between mean annual duration of flow as a function of watershed area, and of the relationship between duration of inundation or flow as a function of percent of normal annual precipitation. **A**: Mean annual duration of flow as a function of watershed area for the seven selected watersheds (Table 3) in the same physio-graphic region as Coyote Creek watershed. **B**: Duration of inundation in a vernal pool (Location 1: top, blue circles) and duration of flow in the draining swale (Location 2: bottom, green squares) as a function of percent of normal annual precipitation

Table 4 Total annual precipitation, percent of normal annual precipitation, total annual duration of inundation in a vernal pool, and total annual duration of flow in the draining swale immediately downgradient of the vernal pool measured between water years 2013–2017 to characterize the relationship between watershed area and mean annual days of flow in the study area (Fig. 5B).

Water Year	Total Annual Precipitation (mm)	Percent of Normal Annual Precipitation	Duration of Inundation in Vernal Pool (days)	Duration of Flow in Draining Swale (days)
2013	411	66%	88	50
2014	370	59%	63	19
2015	457	74%	114	41
2016	609	98%	96	75
2017	706	114%	172	110

the vernal pool and were then translated sequentially downstream, (through its draining swale, to the headwater stream, and so on) with the exception of two peak flows that arrived at location 6 prior to arriving at location 5 (Figs. 6, 7 and 8). Celerities (i.e., the rates of propagation of the pressure heads, in this case the pressure heads of the flood waves) of these nine peak flows varied somewhat across the watershed (Fig. 6). Mean ± SD celerities at interval 1 (i.e., between the vernal pool [Location 1] and its draining swale [Location 2]) were 0.0 ± 0.006 m/s, as the response of the vernal pools and swales to precipitation is almost instantaneous. Between intervals 2 and 5 (i.e., the interval between the swale [Location 2] and the confluence of Coyote Creek with Oat Creek [Location 6]), celerities ranged from a mean ± SD of 0.40 ± 0.3 m/s to 0.16 ± 0.07 m/s, decreasing downgradient through the watershed as slope steepness decreased. At interval 6 (i.e., the interval between the confluence of Coyote Creek with Oat Creek [Location 6] and just above the

confluence of Oat Creek with the Sacramento River [(Location 7]), celerities were a mean ± SD of 0.019 ± 0.01 m/s, a decrease in value as slope is less steep and the Sacramento River contributes to backwater effects at this interval.

Discussion

Vernal pool, swale, and headwater stream complexes are fully integrated into broader flow networks during pronounced wet seasons (Fig. 6). The duration of hydrologic connection within these vernal pool, swale, and headwater stream complexes and to downstream waters varies widely as a function of precipitation, but is ~ 85 days in a normal year in the study area (Fig. 5). While connected, these vernal pool landscapes serve as a prominent source of streamflow to downgradient waters, as storm peaks commonly initiate first in the vernal pools and draining swales, and thereafter
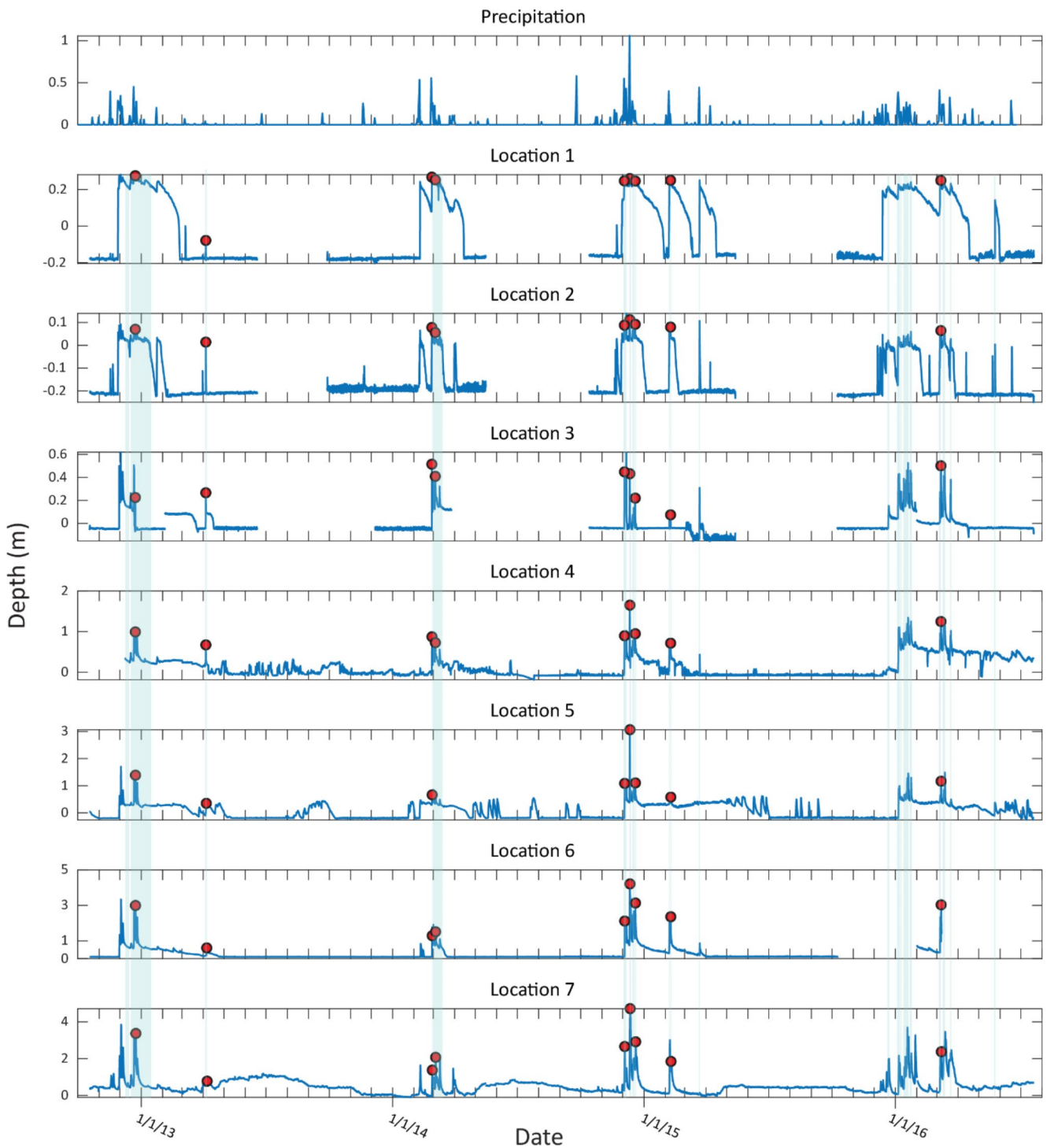
Fig. 6 Precipitation and hydrographs from gages (Locations 1–7) in Coyote Creek watershed. Precipitation (top) and hydrographs showing water levels in the vernal pool (Location 1), its draining swale (Location 2), a series of intermittent draining streams (Locations 3–4), Coyote Creek draining into Oat Creek (Locations 5–6), and ending with the confluence of Oat Creek with the Sacramento River (Location 7). Blue lines indicate stage data (water level) at each gage. Red points indicate peak flows at each location during each of the nine storm events selected for analysis. Intervals with no data reflect time periods when gages were removed. Locations 1–5 each display time periods when water levels appear in the data as below the land surface elevation (values less than 0): these intervals reflect conditions when surface water was lacking, but there was shallow groundwater below the ground surface elevation. Shaded intervals indicate time periods over which all locations were inundated simultaneously

Fig. 7 Precipitation and hydrographs of water level data collected from gages in Coyote Creek watershed for the duration of and following a selected storm event (12/18/2014–12/21/2014). Blue lines indicate stage data at each gage. Red points indicate peak flows at each location during the storm event
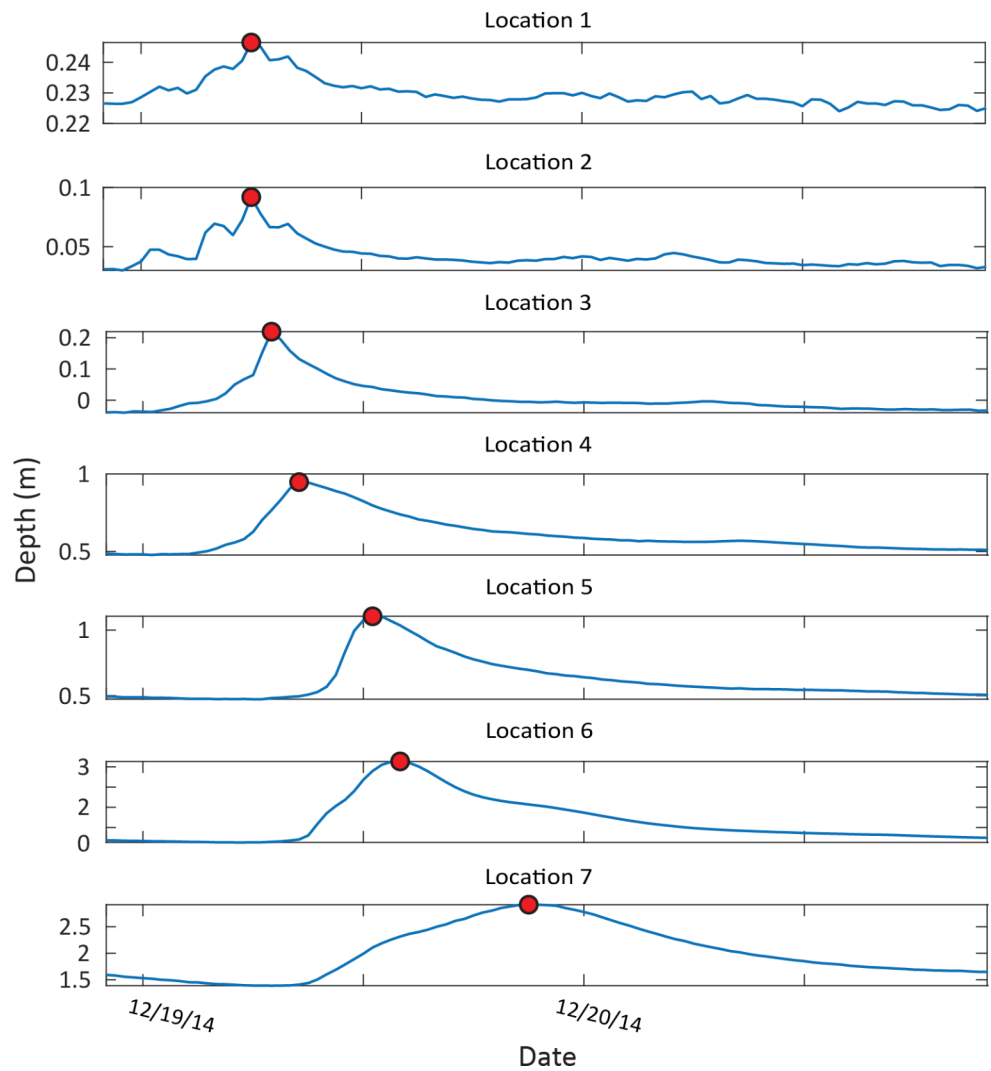
Fig. 8 Average celerities (i.e., the rates of propagation of the pressure heads, in this case the pressure heads of the flood waves) between locations depicted in Fig. 1 during the nine storm events shown on Fig. 6. Intervals on the x-axis represent the sequential intervals between gage locations depicted on Fig. 1 (e.g., interval 1 is between Locations 1 and 2, that is the vernal pool and the draining swale) and therefore do not have units
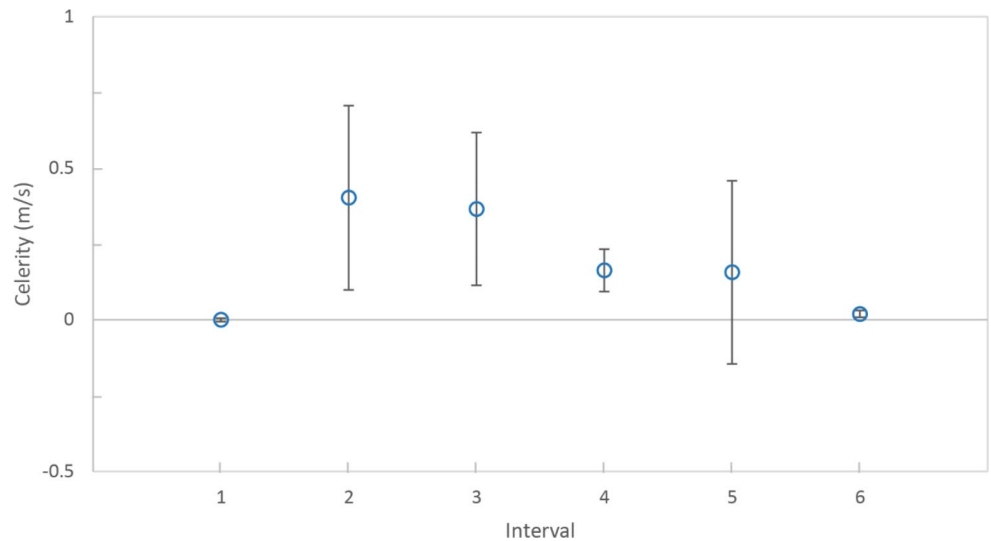
translate to headwater streams and sequentially downstream to the Sacramento River (e.g., Fig. 7).

Vernal pools, swales, and headwater streams connect to each other and to downstream waters as a strong function of precipitation, as a result of minimal surface water and shallow-groundwater storage (Figs. 3 and 4). Vernal pool landscapes are characterized by a lack of water storage capacity due to shallow microtopographic relief and the presence of slowly permeable horizons (Smith and Verrill 1998; Rains et al. 2006, 2008). Local microtopographic relief and the cross-sectional areas of the wetlands and swales are both small, so surface water storage is limited (Fig. 3). Similarly, there typically are multiple slowly permeable horizons within the upper 1–2 m of the soil profile (Fig. 4). This limited surface water and groundwater storage capacity fills rapidly with the onset of the wet season and/or an individual storm (e.g., Rains et al., 2006). Surface water accumulates in the microtopographic lows, which on these vernal pool landscapes are the vernal pools, swales, and headwater streams, and surface water storage begins to reach capacity.

Once storage capacity is exceeded, subsequent precipitation initiates immediate runoff and inundation in the vernal pool, swale, and headwater stream complexes, which is then translated downgradient (Fig. 6). The vernal pool landscapes are nearly level to gently sloping, approaching 0% in some locations (Fig. 3). Additionally, the watershed areas of individual vernal pools are small. Consequently, surface

water flows accumulating within these small watersheds lack sufficient stream power to either erode clear bed and bank features or develop dendritic flow networks. Instead, vernal pools and swales are first interconnected in deranged flow networks, with surface water flowing slowly among the vernal pools and swales, trending downgradient towards the high terrace scarps. Some vernal pools and swales only receive water from their immediate watershed area (i.e., "feeder" vernal pools, *sensu* Bauder [2005]) and other vernal pools and swales receive water from both their immediate watershed area and other upgradient vernal pools and swales (i.e., "collector" vernal pools, *sensu* Bauder [2005]) (Fig. 9). These waters then flow into headwater streams. As a result of these processes, each individual vernal pool and swale contributes differentially to flow generation, with contributions varying in both space and time.

As these waters flow off the high terraces and down the high terrace scarps, combined watershed areas are larger and slopes are steeper, resulting in flows with sufficient stream power to erode stream beds and banks and develop dendritic flow networks (Horton 1945). Once these vernal pools and swales are connected to these headwater streams, they all become part of integrated flow networks. Over the course of the wet season and/or individual storms, these integrated flow networks contribute flow downstream, thereby
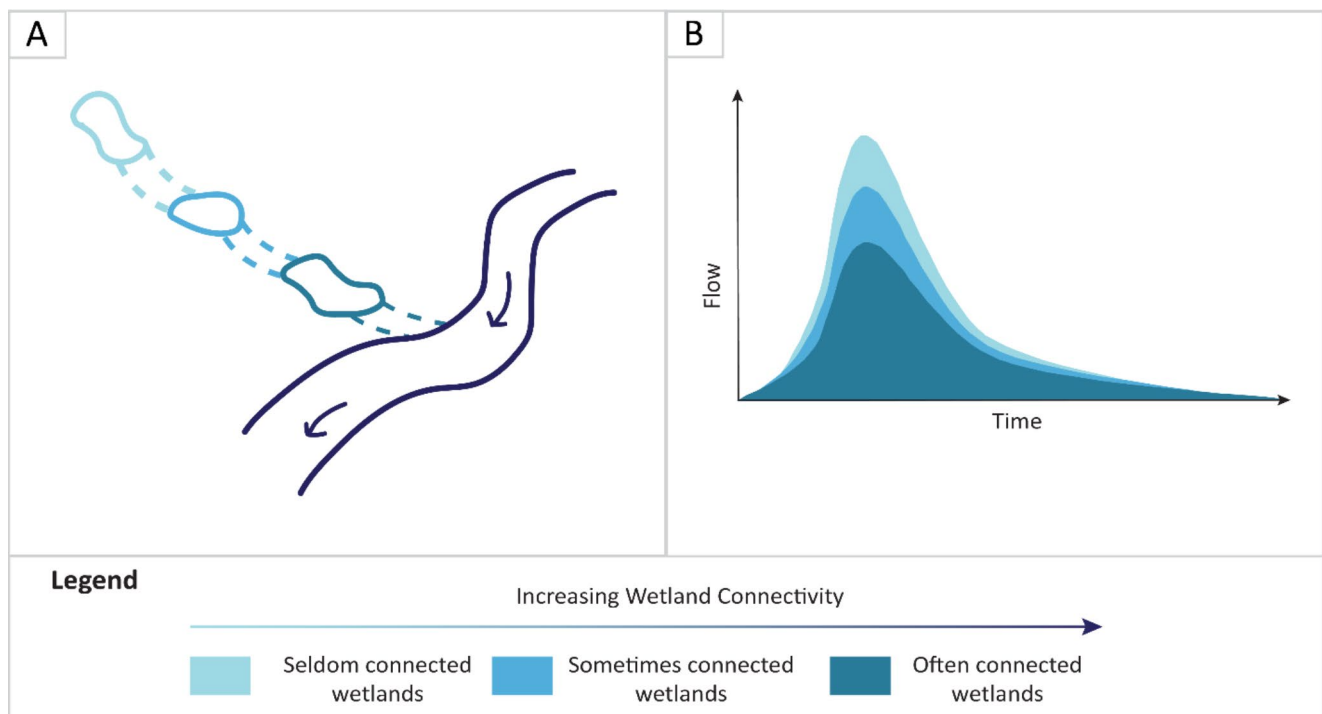

Fig. 9 Illustration of the variable source area effect on the natural flow regime and resulting characteristic hydrograph in an archetypal watershed containing headwater wetlands such as a vernal pool, swale, and headwater stream complex. **A**: The most upgradient wetlands drain downgradient to other wetlands, and downgradient wetlands receive contributions from one or more upgradient wetlands. **B**: At a given time or over a given interval, the effects of headwater wetlands on downgradient hydrographs emerge from the convolution of the hydrographs of the entire system. A convoluted hydrograph is composed of the time-varied contributions from each wetland in the system

comprising the variable source area of downstream waters (e.g., Dunne and Black, 1970; Hewlett and Nutter, 1970).

Vernal pool, swale, and headwater stream complexes exhibit a range of connectivity behavior over the course of the year as a result of the strongly seasonal Mediterranean climate (Fig. 10). Vernal pool, swale, and headwater stream complexes are not inundated during the dry season. They are seasonally and intermittently inundated, but not fully connected, as the wet season begins. As the wet season progresses and the limited soil water storage capacities are exceeded, they become inundated, fully connected, and flowing. As the wet season ends, and evapotranspiration processes are amplified with increasing seasonal heat, they become intermittently inundated and flowing.

Annual precipitation is highly variable in Mediterranean climates (e.g., Bonada and Resh, 2013). We overcame this by collecting data over a period of five years (i.e., October 2012-September 2017). During this time, precipitation ranged from 59 to 114% of normal (Table 4; Fig. 5). This variability is typical, as precipitation ranged from 56 to 187% of normal between 1981 and 2010 (Red Bluff Municipal Airport, Station 24,216, 1981–2010).

The hydrographs of the vernal pool, swale, and headwater stream complexes responded rapidly and linearly to this precipitation (Figs. 6 and 7). Precipitation events, total precipitation volume, and subsequent flow in the vernal pool, swale, and headwater stream complexes tend to occur during concentrated time periods during the wet seasons in this physiographic region (Fig. 6). Therefore, the rapid responses followed by brief recessional limbs in the hydrographs typically link, producing ~85 days of continuous or near-continuous flow from the vernal pool, swale, and headwater stream complexes during a normal year (Fig. 6). As a result of the highly variable amount of annual precipitation in this region, flow from the vernal pool, swale, and headwater stream complexes also varies greatly from year to year. Flow from the vernal pool, swale, and headwater stream complexes ranged from 19 to 110 days during the time period analyzed in this study (Table 4; Fig. 5). If this relationship holds throughout the normal range of precipitation, then flow from the vernal pool, swale, and headwater stream complexes likely ranged from ~20–200 days per year between 1981 and 2010.

Though they constitute a small proportion of watershed area, vernal pool, swale, and headwater stream complexes play a disproportionate role in routing precipitation from the vernal pool landscapes to downstream waters during pronounced wet seasons. Vernal pool landscapes comprise 20%, 8%, and 13% of the Coyote Creek watershed, the Oat Creek watershed, and the total combined watershed areas, respectively (Fig. 2). Similarly, vernal pool, swale, and headwater stream complexes on these vernal pool landscapes comprise 4.0%, 1.6%, and 2.6% of the Coyote Creek watershed, the Oat Creek watershed, and combined watersheds,
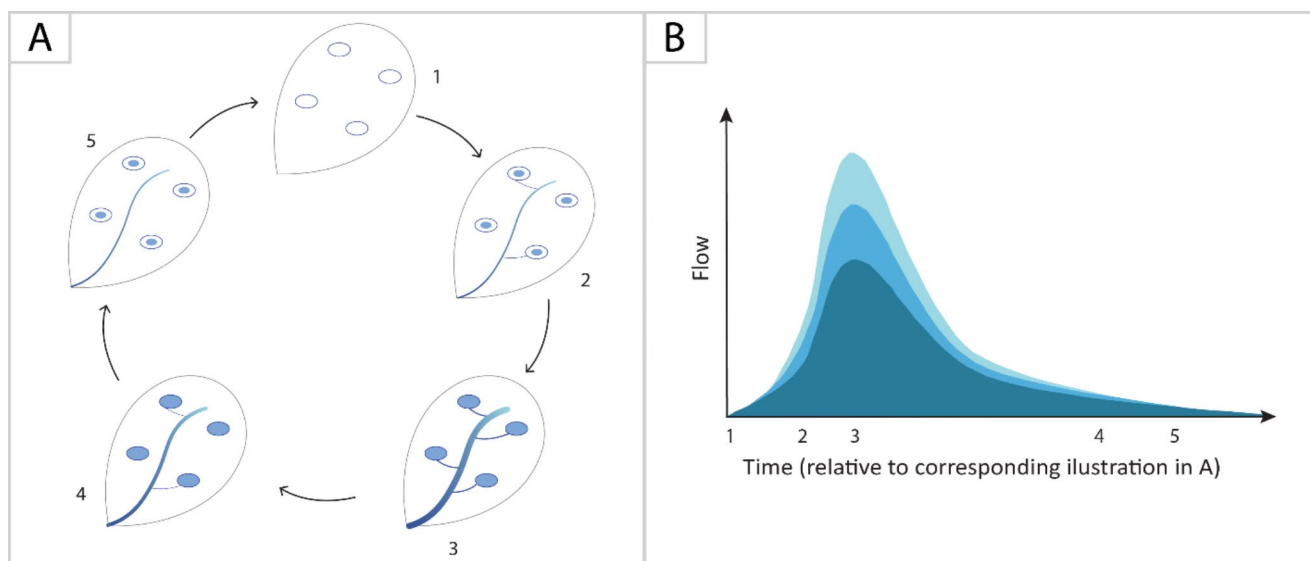

Fig. 10 Illustration of variable source area (VSA) concept in an archetypal vernal pool, swale, and headwater stream complex, and a resulting archetypal hydrograph. The circle of diagrams **(A)** illustrates the annual cycle of wetting and drying of these vernal pool, swale, and headwater stream complexes which function as headwater wetland systems. **A and B: 1**: During the driest parts of a dry season, there is no inundation or flow in the vernal pool, swale, and headwater stream complex. **2**: As the wet season begins, shallow subsurface storage is quickly filled, leading to the initiation of surface inundation and then flow generation and propagation. **3**: During the wettest parts of the wet season, the landscape receives regular precipitation, and subsequently flow through the vernal pool, swale, and headwater stream complex is continuous or nearly continuous. **4**: Late in the wet season, precipitation declines, the vernal pool, swale, and headwater stream complex features become surface-water isolated, and flow generation and propagation decrease. **5**: In the early dry season, some residual moisture remains and inundation persists, but outflow from the vernal pools and swales to the headwater stream complex ceases

respectively (Fig. 2). Our estimates are consistent with other estimates throughout the Central Valley, including those that include the Coyote Creek and Oat Creek watersheds (e.g., Holland 1996; 1998).

Though vernal pool, swale, and headwater stream features are structurally distinct from one another, they are functionally similar and collectively serve as key sources of streamflow when fully connected and flowing during the wet season (Fig. 5). At such times, they act as part of the variable source area for the Coyote Creek and Oat Creek watersheds, as flow peaks appear first on the vernal pool landscapes and are thereafter propagated sequentially and continuously downstream to the Sacramento River (Figs. 6, 7 and 8).

The convolution of flows contributed from the vernal pool, swale, and headwater stream complexes over space and time therefore contributes to the physical integrity of downstream waters. This logic is in line with the conceptual model proposed by Cohen et al. (2016) and extended specifically to flow generation by Rains et al. (2016), in which the convolution of these spatially and temporally varying contributions results in the characteristic natural flow regime, over a range of time periods (e.g., throughout an individual storm, during a single year, and over the course of many years). The cumulative contribution of the vernal pool, swale, and headwater stream complexes to flow generated within a watershed and the resulting hydrograph can be understood by the convolution of all flow and across all travel times to a downstream location (Figs. 9 and 10). The space- and time-integrated contributions to flow generation contribute to the natural flow regime of that system, and in turn, contribute to the maintenance of the chemical, physical, and biological integrity of downstream waters. However, the magnitude of this contribution and the degree to which the size and spatial arrangement of the individual vernal pool, swale, and headwater stream complexes affects these relationships remains to be established.

The results of this study have important implications for land-use management and regulation of activities within vernal pool landscapes. For example, the lack of surface water and shallow-groundwater storage capacity is in part a function of the slowly permeable horizons in upper pats of modal soil profiles (Fig. 4), which is itself a function of the relatively old age of the deposits on which these vernal pool landscapes occur (Helley and Harwood 1985; Smith and Verrill 1998). These features are widely retained because regional land uses have long been little more than grazing of domestic livestock. Ecosystems of the Central Valley evolved in the presence of light to moderate grazing by native ungulates, like the Tule elk (Wagner 1989). Many of the early European settlers in the Central Valley were beneficiaries of the Spanish Land Grants, in which settlers were

granted large tracts of land on which they subsequently grazed cattle (Allen 1935). Today, cattle grazing remains a widespread and economically important land use in the region (Tehama County Department of Agriculture, 2021). However, irrigated agriculture is becoming increasingly dominant, and the two highest value agricultural commodities for the region are now walnuts and almonds, respectively (Tehama County Department of Agriculture, 2021). These deep-rooted trees cannot be grown on these soils with slowly permeable horizons in the upper parts of modal soil profiles. Therefore, to allow production of these crops, soils are first prepared by deep ripping, in which deep working tines are pulled behind heavy equipment to mechanically break up and shatter the slowly permeable horizons, typically including the duripan. This tillage treatment then increases the depth of both water infiltration and root penetration into the subsurface (Hussein et al. 2019). Though data are sparse, deep ripping is specifically designed to have profound and immediate effects on the patterns and rates of the downward movement of water and water storage in ripped soil profiles. Therefore, the result of deep ripping is to have significant and discernable impacts on the local scale patterns of water flow and circulation. At landscape scales, deep ripping significantly impacts processes of flow generation and the resulting downstream natural flow regimes.

The results of this study also have important implications for policy, especially as it relates to the definitions of the geographic extent of Waters of the United States (WOTUS) that are subject to regulation under the Clean Water Act (CWA). The overall goal of the CWA is to "restore and maintain the chemical, physical, and biological integrity of the Nation's waters" (33 U.S.C. § 1251 et seq. [1972])). Crucial to achieving this goal is the role of various definitions of WOTUS as they relate to the establishment of U.S. federal jurisdiction. The federal government has long struggled with the definition of WOTUS. In recent years alone, the Obama administration promulgated the 2015 Clean Water Rule (CWR) (Federal Register Vol. 80, No. 124) which was subsequently rescinded by the Trump administration in 2019 (Federal Register Vol. 84, N0. 204), and the Trump administration promulgated the 2020 Navigable Waters Protection Rule (NWPR) (Federal Register Vol. 85, No. 77) which was subsequently vacated by the courts in *Pasqua Yaqui Tribe v. U.S. Environmental Protection Agency* (2021). Throughout the debate, tributaries to "traditionally navigable waters" (TNWs) have consistently been included as WOTUS. But where do those tributaries begin? Our results show that vernal pool, swale, and headwater stream complexes are important parts of tributary networks, being connected to downstream waters both structurally (e.g., the elements are physically connected to one another, and to downstream waters) and functionally (e.g., water flows between the

elements, and to downstream waters (e.g., Sullivan et al., 2019, 2020)). These vernal pool, swale, and headwater stream complexes perform lag (i.e., detention), sink (i.e., retention), and source (i.e., transmission) functions (Rains et al. 2016), and therefore contribute to the development and maintenance of natural flow regimes (Poff et al. 1997). These contributions, in turn, help "restore and maintain the chemical, physical, and biological integrity of the Nation's waters." In this case, those "Nation's waters" include lower Coyote Creek and Oat Creek, both designated critical habitat for the U.S. federally listed (threatened) Central Valley spring-run Chinook salmon (*Oncorhynchus tshawytscha*) and U.S. federally listed (threatened) Central Valley steelhead (*Oncorhynchus kisutch*).

While the results of this study are centrally about vernal pools, swales, and headwater streams, they nevertheless also have implications for other headwater wetland systems. Hydrologic connectivity between headwater wetlands and downstream waters is controlled by climate, geology, and topography (Winter 2001). Intra- and interannual variability in precipitation, though particularly notable in the Mediterranean climates of west coast vernal pools, swales, and headwater streams, is common to the climates of many other headwater wetland systems (e.g., (Nowicki et al. 2021, 2022). The underlying climatic, geologic, and topographic conditions control watershed wetness, which in turn controls the presence and degree of hydrologic connectivity between headwater wetlands and downstream waters (Cohen et al. 2016; Rains et al. 2016). These myriad headwater wetland systems therefore occupy different spaces on a drought-and-deluge continuum (Euliss et al. 2004), but nevertheless share the fundamental property of intra- and interannual cycles of connection and disconnection. Notable examples include prairie potholes (Leibowitz et al. 2016), Texas Gulf Coast wetlands (Wilcox et al. 2011), Delmarva bays (McDonough et al. 2015), sandhill wetlands (Nowicki et al. 2021, 2022), and more. This has crucially important implications in terms of how we understand and conserve headwater wetlands and the flow networks within which they reside (Nadeau and Rains 2007).

Conclusion

Our work demonstrates that hydrologic flows in the study area landscape are sourced from vernal pool, swale, and headwater stream complexes. These flows are propagated continuously and sequentially downgradient and provide for direct and long-duration connections of vernal pool, swale, and headwater stream complexes to the TNWs of the Sacramento River. Taken alone or in combination with other similarly situated vernal pool, swale, and headwater stream

complexes in the tributary networks of the upper Sacramento River Valley, these hydrologic connections have direct and important influences on the natural flow regime of the Sacramento River and on associated chemical, physical, and biological processes that occur within the Sacramento River ecosystem, which has implications for vernal pool landscapes and other classes of intermittently flowing wetlands across the Central Valley of California and in other physiographic regions.

Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

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