


Linking variability in climate to wetland habitat suitability: is it possible to forecast regional responses from simple climate measures?

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Abstract Temporary wetlands have value to both ecological and social systems. Interactions between local climate and the surrounding landscape result in patterns of hydrology that are unique to temporary wetlands. These seasonal and annual fluctuations in wetland inundation contribute to community composition and richness. Thus, predicting wetland community responses to environmental change is tied to the ability to predict wetland hydroregime. Detailed monitoring of wetland hydroregime is resource-

intensive, limiting the scope and scale of forecasting. As an alternative, we determine which freely available measures of water availability best predict one component of wetland hydroregime, habitat suitability (i.e., the predictability of water in a wetland) within and among geographic regions. We used data from three North American regions to determine the climate index that best explained year-to-year variation in habitat suitability during a key phenological period—amphibian breeding. We demonstrate that simple, short-term climate indices based solely on precipitation data best predict habitat suitability in vernal pools in the northeast, montane wetlands in the west and coastal plain wetlands in the southeast. These

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relationships can help understand how changes in short-term precipitation patterns as a result of climate change may influence the overall hydroregime, and resulting biodiversity, of temporary wetlands across disparate biomes.

Keywords Wetland hydroregime · Climate · Water availability · Annual dynamics · Wetland-breeding amphibians · Habitat suitability

Introduction

The physical and chemical attributes of freshwater wetlands arise from a complex set of interactions between local climate and the surrounding landscape (Kupferberg 1996; Pounds et al. 1999; Brooks 2004; Strayer and Dudgeon 2010; Jackson et al. 2014). The resulting hydroregime (depth, duration, timing, frequency, and predictability of water in a wetland; Greenberg et al. 2015) in turn structures the community composition and species richness of vertebrates, invertebrates and plants inhabiting these wetlands (Schneider and Frost 1996; Brooks 2000; Brooks and Hayashi 2002; Colburn 2004; Sims et al. 2013). Thus, the ability to predict how climate influences the timing, duration and depth of water in wetlands and how that relationship differs across systems is key to predicting year-to-year variation in habitat suitability and forecasting responses of wetland biodiversity to climate change (Krasnostein and Oldham 2004; Calhoun et al. 2017).

One of the primary mechanisms by which climate change will impact amphibians is by altering the hydroregime of wetlands in which they breed (Greenberg et al. 2015). For example, prolonged periods of reduced precipitation or extreme drought may shorten wetland hydroperiod (i.e., the duration of inundation), thereby leading to changes in species occupancy, richness, and abundance (Donald et al. 2011; Scheele et al. 2012; Zipkin et al. 2012; Grant et al. 2013; Walls et al. 2013a; Miller et al. 2018), or reduced breeding probabilities (Church et al. 2007; Kinkead and Otis 2007) and success (Semlitsch et al. 1987; Jansen et al. 2009; Scheele et al. 2012). In turn, the shortening of wetland hydroperiod may result in overall declines in recruitment (Dodd et al. 1993; Dodd 1994; Taylor et al. 2006) or larval survival and adult fitness

(Semlitsch et al. 1988; McMenamin and Hadly 2010; Ficetola and Maiorano 2016). Changes in the timing and frequency of precipitation may also result in changes to species phenology (e.g., Todd et al. 2010; Klaus and Lougheed 2013; Benard 2015). The onset of breeding migrations as well as the emigration of metamorphosed juveniles have been closely tied to local weather patterns in a variety of systems (Hardy and Raymond 1980; Timm et al. 2007; Todd et al. 2010; Ficetola and Maiorano 2016).

Temporary wetlands (also referred to as ‘intermittently inundated,’ ‘seasonal forest ponds,’ or ‘geographically isolated’ wetlands; Tiner 2003; Calhoun et al. 2017) play a critical role in the life-cycle of some wetland-breeding amphibians (e.g., Semlitsch et al. 1996; Skelly et al. 1999; Babbitt et al. 2003) because they dry on a frequent and often regular basis (Calhoun et al. 2017). Large aquatic predators, such as fish, are generally unable to colonize and persist in temporary wetlands due to these discrete periods of inundation and drying (Babbitt et al. 2003; Brooks 2009). In addition to habitat for an assortment of specialized species, temporary wetlands provide a variety of ecosystem services, ranging from flood abatement and water filtration to carbon sequestration and connecting nutrient pools between aquatic and terrestrial systems (Leibowitz 2003; McLaughlin and Cohen 2013; Cohen et al. 2016). Further, temporary wetlands are small in size and often lack surface connections to other water bodies (Leibowitz 2003; Zedler 2003), thereby making them especially sensitive to changes in local temperature and precipitation patterns (Winter and Rosenberry 1998; Winter 2000; Greenberg et al. 2015; Calhoun et al. 2017). This sensitivity, coupled with the vital role these wetlands play in diverse ecosystems, means that our ability to predict responses to year-to-year variation in short-term weather patterns resulting from changes in long-term climate, is critically important for making predictions about the fate of wetland biodiversity under a changing climate (Winter and Rosenberry 1998; Krasnostein and Oldham 2004; Ryan et al. 2014).

Wetland hydroregime is influenced by a combination of edaphic and geomorphic, as well as climatic factors (Winter 2000; Brooks and Hayashi 2002; Grant 2005; Jackson et al. 2014). Consequently, different types of temporary wetlands (e.g., prairie potholes, playas, vernal pools) are likely to respond differently to changing climatic conditions based on local soil

characteristics (e.g., texture, structure, organic matter content), landscape position, and surface topography (Jackson et al. 2014). Furthermore, the frequency and types of hydrologic inputs and outputs to the wetland impact the depth, length and timing of inundation. Vernal pools in the Northeastern U.S., for example, are often inundated for a short, predictable period of time annually (Zedler 2003; Paton 2005) and are closely tied to seasonal interactions between precipitation patterns and evapotranspiration (Zedler 2003; Brooks 2009). Coastal plain wetlands, on the other hand, exist in regimes of high environmental variability (Michener et al. 1997; Walls et al. 2013b) and are likely to respond differently to changes in precipitation than wetlands of the Northeastern U.S., where annual average precipitation patterns have historically been relatively consistent (Brooks 2004). In addition, the physical differences in basin geomorphology and soil properties may result in differences in water-holding capacity and recharge after precipitation events (Winter 2000; Jackson et al. 2014).

Intensive instrumentation and measurement of weather variables and water levels at a fine scale are ideal data for predicting responses in hydroregime to changes in climate (Krasnostein and Oldham 2004; Lee et al. 2015). However, these methods are expensive when replicated on a large scale, thus financial constraints often limit our ability to forecast changes into the future (Matthews 2010) or even predict year-to-year variation in habitat suitability. One solution is to develop predictions for widely available, high-resolution, gridded environmental indices, such as the many metrics of water availability and water-balance that now exist. These include precipitation-based measures such as the standardized precipitation index (SPI; Guttman 1998), simple water balance metrics such as the standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al. 2010), and metrics that incorporate information on regional soil characteristics and processes such as the Palmer drought indices (Palmer 1965) and variable infiltration capacity models (VIC; Liang et al. 1994). Geospatial data sets exist for each and most can be forecasted based on future climate scenarios using readily available outputs such as precipitation and temperature. At the same time, none of these metrics were specifically developed for temporary wetland systems, and instead focus on measuring stream flow, drought, fire potential, and other variables also related to

environmental water balance, which may limit the ability to predict changes in the different components of temporary wetland hydroregime based solely on climate data sets.

We focused on predicting one component of wetland hydroregime—habitat suitability (i.e., the predictability of water in the wetland) defined by metrics such as the presence or absence of water or wetland size (e.g., maximum depth, area), during the amphibian breeding season. Our goal was to determine whether climate indices related to water availability could predict year-to-year fluctuations in habitat suitability, and whether similar measures worked across wetlands in diverse landscapes. We focused on three distinct North American ecosystems (Fig. 1): vernal pools in the Northeast, montane wetlands in the West, and coastal plain wetlands in the Southeast. We predicted that both vernal pools and coastal plain wetlands would be most sensitive to changes in short-term precipitation. In contrast, we predicted that long-term indices of hydrologic condition or indices that directly measured snowpack, an important component of the hydrologic cycle in montane ecosystems (Cooper 1990; Carroll and Cressie 1997; Ryan et al. 2014), would best explain year-to-year variation in montane wetland suitability. By achieving our goals, we hoped to improve the understanding of how changes in precipitation patterns because of climate change may influence the overall hydroregime, and resulting biodiversity, of temporary wetlands across distinct ecosystems.

Methods

We focused on three geographic regions in which the U.S. Geological Survey's Amphibian and Research Monitoring Initiative (ARMI) had conducted independent, long-term studies on wetland-breeding amphibians. Within each of these regions, surveys were regularly conducted to estimate amphibian abundance or occurrence dynamics. Metrics such as the presence or absence of water or wetland size (e.g., maximum depth, area) were also collected at the time of these surveys as measures of habitat suitability for wetland-breeding amphibians (Table 1). Here, we concentrated on these proxy variables of wetland depth, area and the presence or absence of water, and did not utilize species-specific survey data.

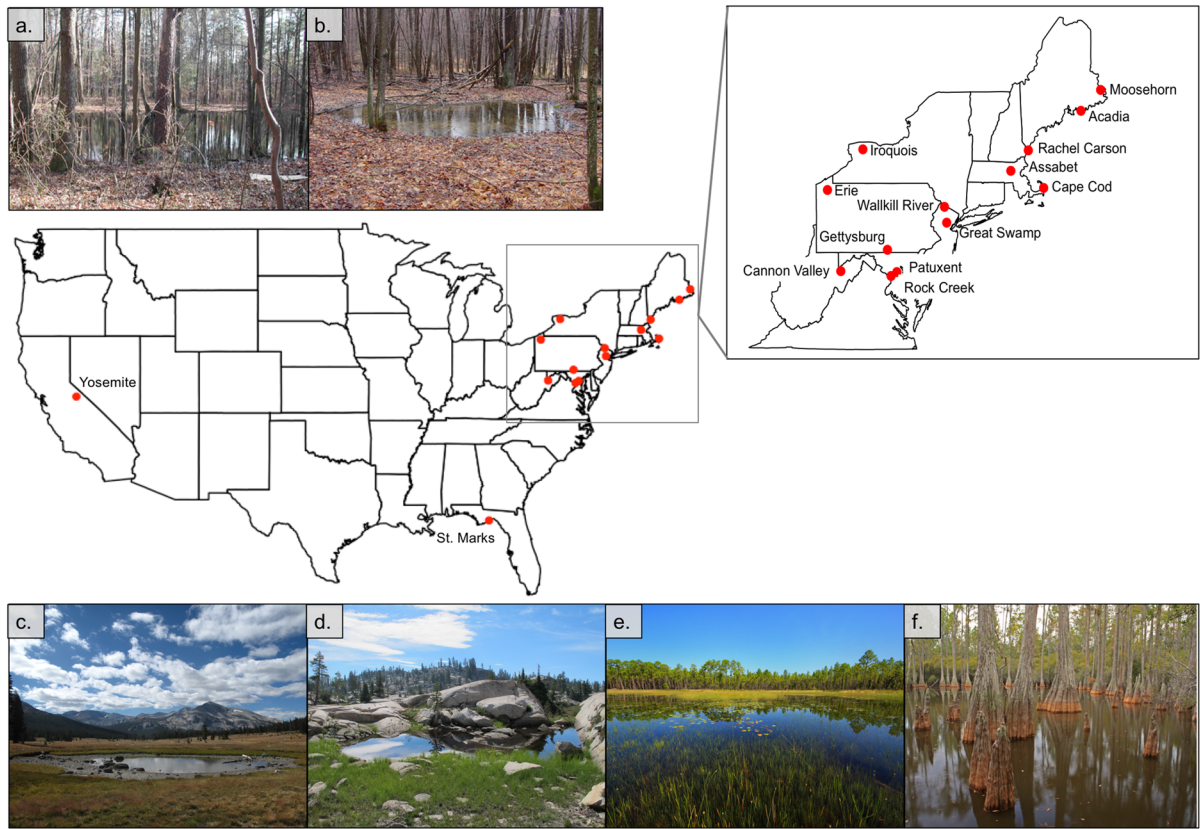


Fig. 1 Map of our three regional study systems located in **a**, **b** 13 National Parks and National Wildlife Refuges in Northeastern U. S., © USGS.; **c**, **d** Yosemite National Park,

CA, in Western U.S., © Jane Lester and Devin Edmonds; and **e**, **f** St. Marks National Wildlife Refuge, FL, in Southeastern U.S., © Alan Cressler

Table 1 Description of the wetland type, response variable, and the method of data collection for each region

Region	Wetland type	Response variable	Method of collection
Northeastern U.S.	Vernal pools	Wetland depth	Maximum depth averaged over all visits within the same sampling window
Western U.S.	Montane wetlands	Wetland area	Width and length measurements taken at furthest points of the visible water line
Southeastern U.S.	Coastal plain wetlands	Proportion of wetlands dry	Presence or absence of water in wetland; sampled in both spring and fall seasons

Region #1: Vernal pools in Northeastern U.S.

We used data collected from $n = 370$ wetlands throughout 13 National Parks (NP) and National Wildlife Refuges (NWR) throughout the Northeastern U.S. (Fig. 1a, b), where vernal pools have been well studied (see Crouch and Paton 2002; Calhoun et al. 2003; Egan and Paton 2004; Paton 2005) and are

abundant, accounting for approximately 57% of all wetlands (Paton 2005). We limited our analysis to the subset of monitored wetlands visited ≥ 3 years between 2004 and 2014 (Online Resource 1). Data were comprised of observations from: Acadia NP, ME ($n = 22$ wetlands), Assabet River NWR, MA ($n = 20$), Cape Cod National Seashore, MA ($n = 30$), Canaan Valley NWR, WV ($n = 49$), Erie NWR, PA ($n = 18$),

Gettysburg National Military Park, PA ($n = 21$), Great Swamp NWR, NJ ($n = 41$), Iroquois NWR, NY ($n = 20$), Moosehorn NWR, ME ($n = 20$), Patuxent Research Refuge, MD ($n = 84$), Rachel Carson NWR, ME ($n = 12$), Rock Creek NP, DC ($n = 9$), and Walkill River NWR, NJ ($n = 24$). In all study areas, annual mean precipitation during the 2004–2014 sampling period was consistent with, or slightly higher than, the climate normal for mean annual precipitation (i.e., 30-year mean; Table 2).

We restricted our analysis to spring sampling occasions (i.e., March–May), during which time amphibians were breeding and laying eggs. We measured maximum wetland depth during each visit and averaged measurements across all visits within our March–May sampling window because individual sites were often surveyed more than once during this time. We further standardized all measurements for each wetland to have a mean of zero across all years,

thus allowing us to focus on temporal rather than spatial variation in maximum wetland depth.

Region #2: Montane wetlands in Western U.S.

For region #2, we used data collected from $n = 85$ wetlands in Yosemite NP (Fig. 1c, d). Sites were annually sampled from June to August along an elevation gradient (ranging from 2240 to 3012 meters) between 2007 and 2015 (Online Resource 1). Mean annual precipitation during the sampling period (2007–2015) was slightly lower than the region's climate normal (Table 2), but variability between years in mean annual precipitation was high.

We measured wetland area using width and length measurements taken at the furthest points of the visible water line. We standardized area measurements for each wetland to have a mean of zero meters across all years, which allowed us to control for spatial (or elevational) patterns in wetland dynamics. To account

Table 2 Annual mean precipitation climate normal and mean annual precipitation for each study area, with their respective standard deviations

Study area	Climate normal precip. ^a (cm)	Mean annual precip. ^b (cm)	SD
Region #1: Northeastern U.S.			
Acadia NP, ME	10.28	11.51	1.59
Assabet River NWR, MA	10.19	10.78	1.47
Cape Cod National Seashore, MA	10.26	10.83	1.08
Canaan Valley NWR, WV	10.36	10.34	0.86
Erie NWR, PA	9.41	9.91	1.03
Gettysburg National Military Park, PA	8.93	9.57	1.18
Great Swamp NWR, NJ	10.29	10.81	1.72
Iroquois NWR, NY	8.47	8.94	0.64
Moosehorn NWR, ME	9.74	10.84	1.45
Patuxent Wildlife Research Center, MD	9.20	9.50	1.26
Rachel Carson NWR, ME	10.28	11.51	1.59
Rock Creek NP, DC	9.20	9.50	1.26
Walkill River NWR, NJ	10.29	10.81	1.72
Region #2: Western U.S.			
Yosemite NP, CA	4.43	3.40	1.35
Region #3: Southeastern U.S.			
St. Marks NWR, FL	12.34	12.29	2.31

Mean precipitation records for each climate division, retrieved from nClimDiv

^aRepresents a 30-year (1981–2010) mean of annual precipitation

^bMean annual precipitation calculated from 2004 to 2014 in the Northeastern U.S., 2007–2015 in the Western U.S., and 2009–2014 in the Southeastern U.S.

for year-to-year variability in sampling date among sites, we also included a standardized effect for Julian date in all models.

Region #3: Coastal plain wetlands in Southeastern U.S.

We used data collected from St. Marks NWR, FL comprised of observations from $n = 60$ wetlands in the refuge's Panacea Unit from 2009 to 2014 (Fig. 1e, f). Surveys were conducted during both the spring (March–April) and fall (September–October) breeding seasons at 45 wetlands from 2009 to 2011, and an additional 15 sites from 2012 to 2014 (Online Resource 1; Walls et al. 2013a). All climate data were retrieved for the months of April and October for spring and fall sampling occasions, respectively. The sampled interval was punctuated by extensive drought in 2010–2011 and heavy precipitation and flooding as a result of Tropical storm Debby in 2012 (see Walls et al. 2013a; Davis et al. 2017). However, annual mean precipitation during the overall sampling period (2009–2014) did not differ from the region's climate normal (Table 2).

Measurements of wetland area or depth were not taken at the time of amphibian surveys in this study area. Instead, we focused on the presence or absence of water in a wetland during amphibian breeding seasons (i.e. was a wetland suitable habitat for breeding to occur). Consequently, our response variable was the proportion of monitored wetlands that were dry in each sampling period. We analyzed spring and fall sampling occasions independently to understand seasonal differences in the index that best captures variability in year-to-year habitat suitability.

Climate index covariates

We focused on a set of readily available indices (Table 3) which have been successfully used by ecologists to relate wetland hydroregime to species occurrence patterns (see Walls et al. 2013a; Davis et al. 2017; Miller et al. 2018 for examples). These indices include the: Palmer hydrological drought index (PHDI), Palmer drought severity index (PDSI), Palmer modified drought index (PMDI), Palmer Z index (ZNDX; also known as the Palmer moisture anomaly index) and a suite of standardized precipitation indices (SPI; calculated over 1-month, 2-month,

3-month, 6-month, 9-month, 12-month and 24-month time intervals). Area-specific data were retrieved from the nClimDiv dataset, compiled by National Oceanic and Atmospheric Administration according to climate division (NOAA's Gridded Climate Divisional Dataset 2015; Vose et al. 2014). A list of the area-specific climate divisions is presented in Online Resource 2. Note that the Northeastern U.S. region included multiple climate divisions, while the Western and Southeastern U.S. regions each only included one division. Therefore, we use the term 'region' to refer to the general location of our study sites in the Western and Southeastern U.S. but acknowledge that our inferences are limited to the level of the climate division for these two regions where data were spatially sparse. All climate indices were calculated monthly; values were retrieved for the middle of the sampling window when most surveys were conducted in each region. This corresponded to the months of April and July for the Northeastern and Western U.S. regions, respectively. For the Southeastern U.S. region, this corresponded to the months of April for the spring and October for the fall sampling occasions.

Each of these indices examines deviations from a site's average precipitation. For example, PHDI measures hydrological impacts (e.g., reservoir and groundwater levels) of prolonged drought conditions (Karl 1986; Guttman 1991), while PDSI examines consequences of meteorological drought. PDSI can respond much more rapidly to changing conditions, as hydrological impacts of drought (measured by PHDI) take longer to recover than meteorological impacts (Palmer 1965; Alley 1985). PHDI and PDSI make use of precipitation and surface air temperature in a physical water-balance model, thus capturing changes in potential evapotranspiration (Palmer 1965; Heim 2002; Dai et al. 2004). However, PDSI does not account for the delayed effects of runoff due to snow melt, for example, and does not adequately capture droughts on time scales less than 12 months (Heim 2002). PMDI is a weighted average of the measures used to calculate PDSI and is equivalent to PDSI during established droughts or 'wet' periods, but differs during transition periods (Heddinghaus and Sabol 1991). Similarly, ZNDX can also be derived from the calculation of PDSI but examines monthly moisture dynamics, thus capturing short-term departures from normal precipitation patterns (Sakamoto 1978; Karl 1986; Heim 2002; Dai et al. 2004).

Table 3 Description of the 6 readily available indices related to water availability that we used to explain annual variation in temporary wetland inundation in three distinct North American ecosystems

Index	Description	References
Palmer's drought severity index (PDSI)	Measures meteorological drought; takes into account precipitation, evapotranspiration, soil-moisture conditions	Palmer (1965); Alley (1985)
Palmer's hydrological drought index (PHDI)	Measures hydrological impacts of prolonged drought conditions; takes into account precipitation, evapotranspiration, soil-moisture conditions	Karl (1986); Guttman (1991); Palmer (1965)
Palmer's modified drought index (PMDI)	Weighted average of the measures used to calculate PDSI	Heddinghaus and Sabol (1991)
Palmer's Z index (ZNDX)	Derived from the calculation of PDSI; captures monthly moisture dynamics	Sakamoto (1978); Karl (1986)
Standardized precipitation index (SPI)	Based on the cumulative probability of a rainfall event occurring; only quantifies hydrologic inputs to the system; calculated over 1-, 2-, 3-, 6-, 9-, 12-, 24-month intervals to capture short or long-term effects	Guttman (1998)
Snow water equivalence (SWE)	Measures the amount of water contained within the snowpack	Jonas and Magnusson (2009)

The standardized precipitation index is the simplest of these indices because it only quantifies hydrologic inputs to the system (Guttman 1998). SPI is standardized so that a value of 0 indicates a site received the median amount of precipitation, as calculated over at least a 30-year period (Guttman 1998). Deviations from 0 are reflected as standard deviations from the long-term average. SPI can be calculated for different time intervals to reflect short (e.g., 1-month; SPI-01) and long-term (e.g., 24-month; SPI-24) impacts of deviations from a site's average precipitation. This allows for drought conditions to be experienced over one time scale (i.e., in the short term) but not over another (i.e., the long term). We included SPI calculated over 1-month, 2-month, 3-month, 6-month, 9-month, 12-month and 24-month time intervals as potential explanatory variables.

We included additional climate covariates for our montane study system that captured snow water equivalence (SWE), which measures the amount of water contained within the snowpack (Jonas and Magnusson 2009). We used data from the Snow Telemetry Network (SNOTEL), which consists of over 800 high-elevation sites monitored throughout the Western U.S. Data on snowpack, precipitation and temperature are collected in a standardized manner across all SNOTEL sites. Products derived from SNOTEL data are common and widely available across the Western U.S., thus facilitating their use in large-scale ecological studies. However, only one

SNOTEL site (#846; Snow Telemetry and Snow Course Data and Products) was located within the Yosemite NP study area. Therefore, we retrieved daily SWE data for this single, centralized location (#846) and summarized those data to capture annual maximum (MaxSWE) and mean (MeanSWE) values applicable to the entire study area. While this is a coarse measure of SWE at the wetland-level, this measure was comparable to all of our other climate indices that were calculated at the level of a climate division. Furthermore, the use of standardized SNOTEL data, as opposed to other measures of snowpack, increases the applicability of our approach outside of Yosemite NP.

Statistical estimation

All statistical models were fit in R (R Core Team 2017). We analyzed data using linear regression for the Northeast vernal pool and Western montane systems, and logistic regression for our Southeast coastal system. We report estimates from the 'best-fit' models for each region, as selected via Akaike's Information Criterion (AIC) and set statistical significance at an α -level = 0.05.

Our interest in this study was our ability to explain year-to-year variation in habitat suitability, as defined by the metrics of wetland size (e.g., maximum depth, area) or the presence or absence of water during the amphibian breeding season. Our observations

included additional sources of variation, which needed to be accounted for when assessing model fit. These additional sources of variation can be decomposed within each region into the heterogeneity among individual wetlands, between years, and the interaction between these two effects (Whittaker 1984; Grömping 2007). To measure fit in the component we were interested in, we first decomposed the overall variance (e.g., Cushman and McGarigal 2002; Lawler and Edwards Jr. 2006; Grömping 2007) to isolate year-to-year effects and measure variation explained in this component (Online Resource 3). We report R^2 values for our linear models as a proportion of the year-to-year variation explained by the ‘best-fit’ climate index in the Northeastern and Western regions. For the Southeastern study region, we report McFadden’s pseudo R^2 (R^2_{McFadden} ; McFadden 1974) as a measure of explained variability in our ‘best-fit’ logistic model. McFadden’s pseudo R^2 compares the maximized log likelihood for an intercept-only model to the model fit with the ‘best-fit’ climate index. Values of R^2_{McFadden} between 0.2 and 0.4 are indicative of good model fits (Domencich and McFadden 1975; McFadden 1977).

Results

Region #1: Vernal pools in Northeastern U.S.

Short-term indices performed best at capturing variability in maximum depth across all 13 study areas in the Northeastern U.S. Specifically, SPI calculated over a 6-month time interval (SPI-06) best explained variation in maximum wetland depth (Table 4). On average, wetland depth increased in years with above average precipitation and decreased during periods of drought [$\hat{\beta}$ (95% CI) 0.02 (0.01, 0.03); Fig. 2a]. $R^2 = 0.40$ (p value < 0.001) when measuring the amount of among-year variation explained by SPI-06.

Region #2: Montane wetlands in Western U.S.

The standardized precipitation index calculated over a 3-month time interval (SPI-03) best explained year-to-year variation in wetland area for Yosemite NP (Table 4). Contrary to our predictions, MaxSWE and MeanSWE performed poorly relative to all other indices, with the exception of SPI-24. In fact, all of our

long-term metrics performed poorly when compared to the Standardized Precipitation Indices. The positive relationship between SPI-03 and wetland area was statistically ‘significant’ [$\hat{\beta}$ (95% CI) 245.08 (167.29, 322.86), p value < 0.001; Fig. 2b] with an $R^2 = 0.40$ for the among-year component of variation. Despite site-level heterogeneity, observed values of PHDI, PDSI and ZNDX retrieved from nClimDiv at the climate division-level did not differ during the study period. Our models and resultant estimates are therefore identical for these three indices (see Table 4).

Region #3: Coastal plain wetlands in Southeastern U.S.

Short-term indices also performed best at capturing year-to-year variation in the presence of water in the basin, for both seasons at SMNWR. The proportion of wetlands dry at the time of sampling was most closely related to SPI calculated over a 2-month [SPI-02; $\hat{\beta}$ (95% CI) – 1.76 (– 0.60, – 2.91)] and 3-month [SPI-03; $\hat{\beta}$ (95% CI) – 0.60 (– 0.30, – 0.90)] time interval for spring and fall occasions, respectively (Table 4). Each of these indices was negatively correlated with the proportion of wetlands dry for amphibian breeding at the time surveys were conducted (Fig. 2c, d). Furthermore, these predictors captured a high proportion of variability in this response variable during both the spring (SPI-02: $R^2_{\text{McFadden}} = 0.43$, p value = 0.003) and fall seasons (SPI-03: $R^2_{\text{McFadden}} = 0.39$, p value < 0.001).

Discussion

In each of our three North American ecosystems, we demonstrate that habitat suitability (measured by maximum depth, area and presence or absence of water—important metrics for amphibian breeding and recruitment) is most sensitive to changes in short-term precipitation. The standardized precipitation indices are the simplest of our tested climate variables (Vincente-Serrano et al. 2010), but best predicted year-to-year variability in habitat suitability in all three regions. However, the time scales of these ‘best-fit’ SPI differed among regions and between seasons in the case of our Southeastern U.S. study area. These differences are likely a result of regional and site-

Table 4 Δ AIC values for each study region's regression analysis, relating annual wetland metrics to climate indices

Index	Region #1: Vernal pools	Region #2: Montane wetlands	Region #3a: Coastal plain wetlands (spring)	Region #3b: Coastal plain wetlands (fall)
SPI-01	41.07	18.89	10.25	13.98
SPI-02	20.30	18.19	0.00	10.83
SPI-03	9.70	0.00	10.00	0.00
SPI-06	0.00	8.74	17.58	4.19
SPI-09	35.89	14.55	11.51	9.69
SPI-12	37.30	13.93	10.75	12.92
SPI-24	28.33	32.23	11.38	16.59
ZNDX	20.99	29.53 ^a	7.31	11.82
PDSI	28.12	29.53 ^a	0.15	4.72
PMDI	40.92	5.19	0.05	3.09
PHDI	12.21	29.53 ^a	8.77	8.91
MaxSWE	–	36.87	–	–
MeanSWE	–	33.58	–	–

Bolded values indicate the best-supported models according to AIC

^aNo variation was observed in the values of PHDI, PDSI and ZNDX retrieved from nClimDiv for the study period

specific differences in soil composition, surficial geology, basin geomorphology, and climate that influence the interactions between year-to-year water availability and habitat suitability. Nevertheless, SPI out-performed all other indices, including the short-term Palmer indices, PMDI and ZNDX, that explicitly account for precipitation, evapotranspiration, and soil-moisture conditions. Metrics based only on precipitation data, such as SPI, have been shown to accurately determine the intensity, duration and extent of drought events (Chang and Cleopa 1991; Heim 2002; Vincente-Serrano et al. 2010) as well as estimate soil-moisture dynamics (Sims et al. 2002). In addition, precipitation-based measures require little data beyond historic precipitation records (Guttman 1998; Vincente-Serrano et al. 2010), making them a useful metric to compare the effects of changing precipitation patterns in vastly different ecosystems. Our results further suggest that we can understand year-to-year variation in habitat suitability across different temporary wetland systems with this set of simple variables.

Precipitation is the primary hydrologic input to vernal pools (Zedler 2003; Brooks 2009). SPI-06 captures short-term deviations from a site's average precipitation, as calculated over the previous 6-month period. For our particular analysis, this corresponds to the time period between November and April, which

captures winter and spring precipitation. Losses via evapotranspiration are a strong driver in forested systems, but primarily occur later in the summer when vegetation is abundant and the canopy is full (Brooks 2004). During the time at which sampling occurred, sites had minimal vegetative growth and low seasonal temperatures precluded the loss of water via evaporation. While indices that account for evapotranspiration, such as PHDI or PDSI, may be better able to capture dynamics in wetland hydroperiod later in the season, we were not able to explicitly test this prediction. Importantly, our results suggest that habitat suitability of vernal pools may not be influenced by antecedent hydrologic conditions of previous years, at least during amphibian breeding (i.e., the time of our sampling).

Snowpack is a well-known contributor to surface water in montane wetlands and serves as an essential water storage mechanism across the landscape (Mote 2003; Jonas and Magnusson 2009; Bowling and Lettenmaier 2010; Ryan et al. 2014). Our results, however, do not clearly support this relationship for Yosemite NP. Instead, our results indicate that SPI-03 was better able to explain year-to-year variation in wetland area than either of our two SWE metrics. At the time of sampling (June–August), therefore, wetlands were primarily influenced by precipitation

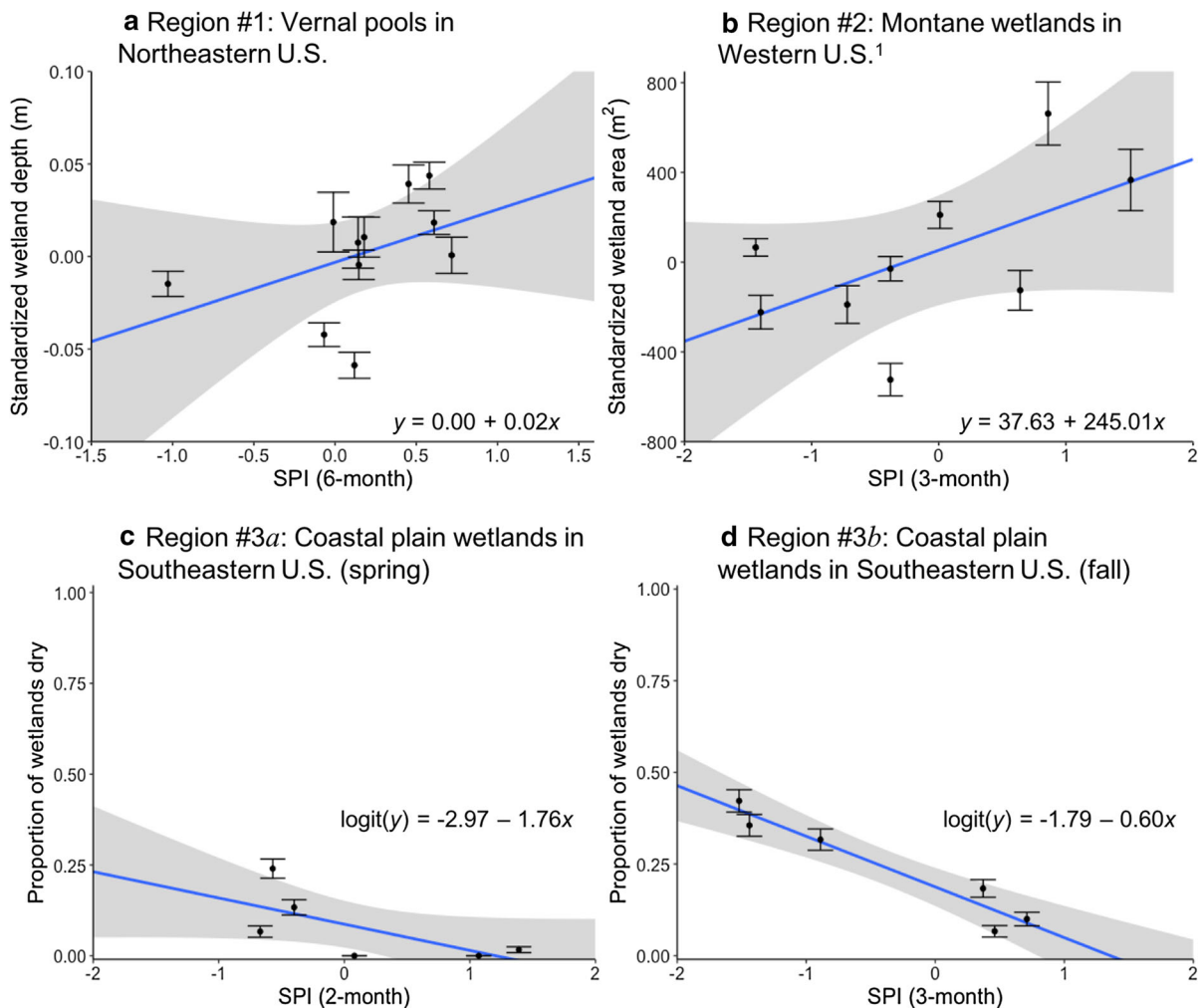


Fig. 2 Annual wetland metrics ($\bar{x} \pm SD$) as a function of the best-fit climate index for temporary wetland systems in **a** Northeastern U.S.; **b** Western U.S.; and **c**, **d** Southeastern

U.S. in the spring and fall seasons, respectively. Blue lines show the estimated relationship and 95% confidence interval for the 'best-fit' climate index and response variable in each region

between April and June. This suggests that either (1) snowpack is not a primary hydrologic driver for our particular set of surveyed wetlands, or (2) there is a great deal of heterogeneity among sites in SWE not captured by the single SNOTEL station used for all sites. At the scale we examined, however, our results suggest that SWE may not be useful for understanding year-to-year site-specific variation in habitat suitability at the onset of amphibian breeding.

Oscillations in water availability have structured coastal landscapes for millennia (Michener et al. 1997). We tested the prediction that habitat suitability in our Southeastern coastal system, as a result, was more correlated with short- rather than long-term

indices. We found this to be an accurate prediction; despite severe drought conditions during the study period, long-term indices were poor predictors of year-to-year habitat suitability. SPI-02 and SPI-03 were highly correlated with our observations of the presence or absence of water in the spring and fall seasons, respectively. Importantly, additional inputs via storm surge or flooding are not captured by SPI, but can influence hydroperiod, wetland productivity, and community composition through a variety of mechanisms (e.g., sediment deposition, salinization; Michener et al. 1997; Herbert et al. 2015; Davis et al. 2017). Our results indicated that PMDI and PDSI were also strongly supported ($\Delta AIC < 2$) in the spring seasons,

further suggesting that factors associated with meteorological drought (i.e., consistent, dry conditions associated with below-average precipitation; Heddinhaus and Sabol 1991) are important to consider when predicting habitat suitability for breeding amphibians in coastal systems.

As a result of climate change, precipitation is predicted to decline in the Southeast and increase in the northeastern U.S. (Dore 2005; IPCC 2014) during the late winter and early spring. These changes in the amount of overall precipitation will undoubtedly shift wetland hydroregime (Brooks 2004; Greenberg et al. 2015). This likely means that many of the wetlands we examined in the southeastern U.S. will no longer be suitable for breeding amphibians (or other wetland inhabitants) in the future, while those wetlands in the northeastern U.S. may increase in maximum spring inundation (at the time of breeding). As a result, many of the ecosystem functions provided by temporary wetland systems may be displaced or lost entirely (Blaustein et al. 2010; Walls et al. 2013b). Specifically, the shortening of wetland hydroperiod due to a decline in overall precipitation may promote early breeding (Beebee 1995; Gibbs and Breisch 2001; Kusano and Inoue 2008) or rapid larval growth and metamorphosis (Wilbur and Collins 1973; Rowe and Dunson 1995), which has been associated with reduced adult fitness (John-Alder and Morin 1990; Goater et al. 1993; Beck and Congdon 2000; Gervasi and Fofopoulos 2008). In contrast, increased precipitation may result in more persistent inundation, thus reducing the habitat that is available and suitable for amphibian species that rely on temporary wetlands (Walls et al. 2013b). Importantly, however, predictions for the northeast also expect more frequent, and more severe, midsummer droughts (Hayhoe et al. 2007), which will reduce probabilities of successful metamorphosis (Mackenzie et al. 2011), leading to an ecological trap. The frequency and types of hydrologic inputs and outputs to the basin impact not only the length but the timing of inundation as well (Pechmann et al. 1989; Babbitt et al. 2003; Colburn 2004; Brooks 2009). In addition to changes in the overall amount of precipitation, temporal changes in weather patterns could also impact the onset, duration and success of seasonal reproduction for wetland-breeding amphibians, though these effects are largely understudied (Walls et al. 2013b). In either case, shifts in the different components of wetland hydroregime across

the landscape would lead to changes in species occupancy (e.g., Raxworthy et al. 2008; Walls et al. 2013a; Miller et al. 2018), community composition (e.g., Babbitt and Tanner 2000), and interspecific interactions (e.g., Davis et al. 2017).

Wetland hydroregime is complex and quantifying system responses to changing conditions is challenging, yet vital to our understanding of how species will respond to climate change (Lee et al. 2015). Our analysis focuses on just one link between climate and hydroregime: the effect of water availability averaged over scales of a couple months to years, interpolated across large spatial scales, and measured at a specific point within an annual cycle. As such, our study does not replace the intensive data collection that characterizes most site-intensive hydrological studies (e.g., Chandler et al. 2017). Our results indicate that while short-term climate indices performed best of the selected indices, these measures still did not capture a large portion of the observed variability in Northeast vernal pools or montane wetlands. Available climate measures, such as those we examined here, may not be at a scale that is useful or adequate for temporary wetlands in these systems. In addition, landscape-level differences in topography and geology, as well as fine-scale differences in basin geomorphology, and soil properties within each study area, likely play an important role that we did not examine here. Future work should focus on better incorporating wetland-level variation and exploring alternative variables that best relate hydrologic inputs to hydroregime and the resultant ecological processes (Brooks and Hayashi 2002). For example, large rainfall events may increase connectivity, allowing aquatic predators to colonize isolated wetlands (e.g., Davis et al. 2017), or otherwise alter habitat suitability for breeding, but we were not able to examine these effects in this study. Future work should also look at the direct and indirect influences of changes to the frequency and timing of large rainfall events on wetland hydroregime throughout the amphibian breeding season, especially because extreme precipitation events are predicted to increase in frequency and/or magnitude across the continental U.S. (Easterling et al. 2000; Allan and Soden 2008).

The ability to link fluctuations in water availability to hydroregime is vital for predicting how wetland community assemblages will respond to environmental change. Understanding these links, however, is complicated by our uncertainties in how climate and

hydrology are linked, and imprecision in measuring relevant local climate and hydrologic dynamics (Winter 2000). This is especially relevant when trying to predict changes in hydrology across expansive landscapes, or even year-to-year variation in habitat suitability. We have demonstrated that there is utility in understanding how coarse measures of water availability will change in the future. However, we have also shown that there is a need to understand the site-specific differences in soil composition, basin geomorphology, and climate that likely resulted in region-level heterogeneity in the time scale over which the ‘best-fit’ SPI was calculated. Despite this, simple metrics such as SPI that are widely available and straightforward to calculate are relevant when the goal is to make landscape-level predictions on the hydrological responses of these important wetland ecosystems to changing climate.

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