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Identifying climate-resistant vernal pools: Hydrologic refugia for amphibian reproduction under droughts and climate change

Jennifer Cartwright¹  | Toni Lyn Morelli²  | Evan H. Campbell Grant³ 

¹US Geological Survey, Lower Mississippi-Gulf Water Science Center, Nashville, Tennessee, USA

²US Geological Survey, Northeast Climate Adaptation Science Center, Amherst, Massachusetts, USA

³US Geological Survey, Patuxent Wildlife Research Center, Turners Falls, Massachusetts, USA

Correspondence

Jennifer Cartwright, U.S. Geological Survey, Lower Mississippi-Gulf Water Science Center, 640 Grassmere Park, Suite 100, Nashville TN 37211.

Email: jmcart@usgs.gov

Funding information

US Geological Survey Northeast Climate Adaptation Science Center

Abstract

Vernal pools of the northeastern United States provide important breeding habitat for amphibians but may be sensitive to droughts and climate change. These seasonal wetlands typically fill by early spring and dry by mid-to-late summer. Because climate change may produce earlier and stronger growing-season evapotranspiration combined with increasing droughts and shifts in precipitation timing, management concerns include the possibility that some pools will increasingly become dry earlier in the year, potentially interfering with amphibian life-cycle completion. In this context, a subset of pools that continues to provide wetland habitat later into the year under relatively dry conditions might function as ecohydrologic refugia, potentially supporting species persistence even as summer conditions become warmer and droughts more frequent. We used approximately 3000 field observations of inundation from 449 pools to train machine-learning models that predict the likelihood of pool inundation based on pool size, day of the year, climate conditions, short-term weather patterns, and soil, geologic and landcover attributes. Models were then used to generate predictions of pool wetness across five seasonal time points, three short-term weather scenarios and four sets of downscaled climate projections. Model outputs are available through a website allowing users to choose the inundation thresholds, time points, weather scenarios and future climate projections most relevant to their management needs. Together with long-term monitoring of individual pools at the site scale, this regional-scale study can support amphibian conservation by helping to identify which pools may be most likely to function as ecohydrologic refugia from droughts and climate change.

KEYWORDS

amphibians, climate change, drought, machine learning, refugia, vernal pools

1 | INTRODUCTION

Climate change poses major threats to global biodiversity and evidence is mounting that amphibians are disproportionately impacted (Miller et al., 2018; Sodhi et al., 2008; Wake & Vredenburg, 2008).

Climate-related threats to amphibians are often compounded by destruction and fragmentation of wetland habitats, degradation of water quality, invasive species, and diseases such as chytridiomycosis (Daszak et al., 2005; Evans et al., 2017; Trauth et al., 2006; Wake & Vredenburg, 2008). Climate-induced hydrologic changes are likely to

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be among the greatest threats to many amphibian populations over the coming decades (Miller et al., 2018; Ray et al., 2016; Scheele et al., 2012). Climate projections in many parts of the world indicate hotter and longer growing seasons coupled with intensification of both heavy precipitation events and droughts (Ahmadalipour et al., 2017; IPCC, 2013; Trenberth et al., 2013; USGCRP, 2018). These changes have potential to degrade amphibian habitat suitability and persistence, especially for species whose recruitment depends on climate-sensitive wetlands (Walls et al., 2013).

Seasonally inundated ponds provide critically important breeding habitat to a wide variety of amphibian species (Semlitsch & Skelly, 2008), including threatened and endangered species in North America (e.g., *Ambystoma cingulatum*, *Ambystoma bishopi*, *Rana sevosia*, and *Pseudacris streckeri illinoensis*; Chandler et al., 2017; Palis et al., 2006; Richter et al., 2003; Trauth et al., 2006) and globally (e.g., *Pseudophryne pengillyi*; Scheele et al., 2012). In the northeastern United States, vernal pools—sensu Zedler (2003), also known as seasonal forest ponds (Brooks, 2000) or ephemeral forest pools (Brooks, 2009)—are small, geographically isolated wetlands that fill from fall through early spring and generally become dry by mid-to-late summer (Leibowitz & Brooks, 2007). The amount of time a vernal pool is available for amphibian breeding, and larval development can range from several weeks to most months of the year; however, annual drying in most years prevents establishment of predatory fish populations (Calhoun et al., 2014; Leibowitz & Brooks, 2007).

The reproductive success of pool-breeding amphibians is closely linked to pool hydroperiod (annual duration of inundation) and to the rate and seasonal timing of pool drying (Chandler et al., 2017; Green & Bailey, 2015). Although amphibian species differ somewhat in their wetland habitat requirements and reproductive phenology, all species have certain minimum hydroperiods required for successful reproduction and larval development (Brooks, 2004; Paton & Crouch, 2002). As a result, pool-breeding amphibians are especially vulnerable to climate-driven hydrologic changes that affect seasonal availability of inundated breeding habitat (Chandler et al., 2016; Green et al., 2013; Ray et al., 2016; Walls et al., 2013). Droughts can shorten pool hydroperiods, causing pools to fill incompletely and/or to dry more rapidly than normal (Brooks, 2004; Werner et al., 2009). These drought effects can reduce amphibian reproductive output and, in some cases, lead to recruitment failure (Chandler et al., 2017; Palis et al., 2006; Scheele et al., 2012; Seigel et al., 2006). Many pool-breeding amphibians are adapted to interannual variability in hydroperiod, and populations may persist through the years of catastrophic reproductive failure (Kinkead & Otis, 2007; Taylor et al., 2006). However, climate-change-induced increases in the number of years with reproductive failure could adversely impact populations over time (Chandler et al., 2016). Indeed, population declines in several species of pool-breeding amphibians have been attributed to climate-induced reproductive failure (Daszak et al., 2005; Scheele et al., 2012; Trauth et al., 2006).

Climate change can alter the hydrology of vernal pools through processes that govern both water inputs and losses. Because pool

filling and maintenance of water levels are often strongly coupled with the timing and amount of precipitation, vernal-pool availability for amphibian breeding may be sensitive to changes in precipitation magnitude and timing—including more intense storm events separated by longer dry periods—and by snow-to-rain transitions in winter precipitation (Brooks, 2004, 2009; Walls et al., 2013). Water loss from vernal pools occurs primarily through surface evaporation, soil drainage (i.e., shallow groundwater recharge), and lateral water transfers to adjacent uplands to replace soil water lost to transpiration (Brooks, 2009; Leibowitz & Brooks, 2007). The relative importance for pool drying of these water-loss processes depends in part on the geometry and substrate characteristics of pool basins, along with local groundwater characteristics and landcover and topography of the landscapes in which pools are embedded (Brooks & Hayashi, 2002; Calhoun et al., 2014; Jones et al., 2018). Because evapotranspiration is strongly temperature dependent, overall growing-season warming and earlier seasonal temperature increases (i.e., earlier spring increases in evaporative demand, along with earlier leaf-out leading to earlier ramp-up of transpiration) are expected to increase pool-drying rates and have the potential to shift pool-drying dates earlier in the season (Brooks, 2005, 2009; Leibowitz & Brooks, 2007; Rodenhouse et al., 2009). Combined climate impacts on both water inputs to, and losses from, vernal pools have raised concerns about hydroperiod shortening, potentially interfering with amphibian reproduction (Brooks, 2004, 2009; Chandler et al., 2016; Palis et al., 2006; Rodenhouse et al., 2009). However, vernal pools—even those in close geographic proximity—may vary substantially in their hydrologic responses to climate drivers, owing to differences in pool characteristics (e.g., size, morphology and groundwater interactions), as well as in features of their immediate surroundings and the larger landscape (Brooks & Hayashi, 2002; Chandler et al., 2017; Jones et al., 2018; Leibowitz & Brooks, 2007).

Variability in the underlying geomorphology and landscape setting of vernal pools suggests that some pools may be less hydrologically sensitive to climate change than others, for example, less responsive in terms of drying date and hydroperiod. In this context, pools that retain water later in the growing season under adverse climatic conditions (e.g., droughts, longer, and/or hotter growing seasons) may provide hydrologic refugia for pool-breeding amphibians. Hydrologic refugia (Cartwright, Dwire, et al., 2020; McLaughlin et al., 2017) are an important subset of climate refugia more broadly, which are locations that may help buffer natural communities from the effects of climate change (Morelli et al., 2020). Vernal pools that exhibit slower or more gradual hydrologic shifts in response to climate change thus could support species persistence in stochastically variable climate regimes and potentially buy time for more comprehensive management responses to climate impacts (Morelli et al., 2020). While identification of hydrologic refugia is an emerging component of wetland conservation in arid and semi-arid landscapes (Cartwright, Dwire, et al., 2020; Davis et al., 2013; Russell et al., 2020), few studies have sought to identify hydrologic refugia among wetlands in

humid temperate regions, such as vernal pools of the northeastern United States.

We examined the drivers of pool-inundation patterns over the seasonal window associated with pool drying (i.e., late spring through mid-summer) in the northeastern United States. Using approximately 3000 inundation observations from 449 vernal pools located on protected areas across eight northeastern states from West Virginia to Maine, we trained machine-learning models to predict the likelihood of pool inundation based on seasonal timing (Julian day), precipitation inputs and drought indicators, pool characteristics (size and morphology metrics), soil and landscape characteristics, and long-term climate variables. These predictors represented hypothesized relationships drawn from the existing literature on drivers of vernal-pool inundation (Table 1). We then used the models to generate predictions for pool-inundation probability under various scenarios defined by combinations of seasonal time points, weather conditions, and future climate projections. The resulting inundation-probability predictions can be used to identify subsets of pools that might function as hydrologic refugia under a variety of seasonal, weather, and climate contexts, using various thresholds to define vernal pools as refugia (e.g., depending on species of interest). These model predictions can support vernal-pool managers in planning for climate adaptation by suggesting which pools may be most vulnerable to hydrologic effects from climate change—perhaps warranting additional hydrologic monitoring—and, conversely, which pools may warrant further study as potential hydrologic refugia for pool-breeding amphibians.

2 | METHODS

2.1 | Vernal-pool geography

Vernal pools were located across eight states in the northeastern U.S.—from West Virginia to Maine—on 16 ‘units’ (i.e., National Wildlife Refuges, National Parks, and other protected areas; Figure 1). Units contained from 1 to 89 pools (mean = 28 pools per unit). These pools were previously identified using probabilistic sampling methods, described in detail by Van Meter et al. (2008) and summarized briefly here. First, a 500-m grid of points was generated for each unit, and a random sample of points was used to define 50-m by 50-m plots that were visited by field crews in March through June, 2004 and 2005. For each plot in which a pool was found, neighbouring plots were established and searched; this process continued until no additional pools were discovered. Additionally at one unit (Patuxent Research Refuge), leaf-off colour infrared digital photographs were used to identify potential pools, a subset of which was field verified in May through June 2004.

Pools in this study were represented as point locations with horizontal positional accuracy ≤ 10 m. Pool elevation ranged from 1.4 to 1036 m above sea level. Mean annual temperature and mean annual precipitation ranged across units from approximately 4.1°C to 13°C and from 92 to 139 cm, respectively.

2.2 | Pool inundation observations

Pool inundation observations were conducted as part of the US Geological Survey's Amphibian Research and Monitoring Initiative (ARMI) wetland-breeding amphibians surveys. Pools were generally visited between March and July, from 2004 through 2016, though the specific dates varied by latitude according to amphibian breeding phenology (i.e., seasonal timing). At each visit, the inundated width and length of each pool were recorded, from which we calculated

$$A = \frac{\pi LW}{4},$$

where A is the elliptical area as a proxy for pool inundated area, and L and W are pool inundated length and width, respectively (Brooks, 2005). Inundated depth was also recorded at each visit at the deepest point in each pool. Because pools were rarely observed to be dry in March or April and we were primarily interested in dry-down patterns later in the season, we used observations from May through July in inundation modelling ($n = 3004$ observations from 449 pools).

Our dataset did not include geomorphic or bathymetric surveys from which to calculate pool surface area or volume. Therefore, as a rough proxy for pool surface area we calculated mean April inundated area for pools with non-zero April inundation observations. This metric correlated strongly with maximum observed pool inundated area and with mean observed March inundated area (Spearman's $\rho = 0.94$ and 0.92, respectively), suggesting its usefulness as an overall indicator of pool surface area. We calculated pool area-to-depth ratio by dividing average April inundated area by average April inundation depth. Larger area-to-depth ratios generally represent pools with flatter, shallower bathymetry whereas smaller area-to-depth ratios represent deeper, narrower pools.

2.3 | Climate and landscape data

To evaluate the effect of climate-change projections on the hydrology of vernal pools in this study, we compiled 1-km gridded climate variables relevant to climatic water balance for a baseline historical period (1981 through 2010) and projected future time periods (2050s and 2080s) under the Representative Concentration Pathway (RCP) 4.5 and 8.5 greenhouse-gas scenarios from the AdaptWest Project (2015); Table S1. RCP 8.5 generally predicts more rapid climate changes than RCP 4.5, enabling comparison across climate scenarios. Climate variables represented ensembles averaged from 15 downscaled climate models (AdaptWest Project, 2015; Wang et al., 2016). For each unit containing vernal pools used in inundation models, we calculated the percentage change in each climate variable between the baseline and future periods. We represented the distribution of these changes across units using boxplots to assess general trends in climate-change projections.

We represented climatic drivers of pool inundation across three time scales. We deemed it important to include short-term

TABLE 1 Candidate predictor variables for vernal-pool inundation models

Predictor ^a	Category	Units	Dataset type and resolution	Source	Mean (SD) ^b	Hypothesis ^c	References
Julian day*	Time-varying	Day	NA	Pool inundation observation dataset	150.4 (21.2)	Negative	Brooks (2004, 2005); Leibowitz and Brooks (2007)
5-day cumulative antecedent precipitation*	Time-varying	Mm	2.5 arc-minute grid	PRISM daily precipitation dataset (Daly et al., 1994)	17.2 (18.5)	Positive	Brooks (2004, 2005, 2009); Greenberg et al. (2015); Leibowitz and Brooks (2007)
6-month standardized precipitation evapotranspiration index (SPEI)*	Time-varying	Standardized units	2.5 arc-minute grid	WestWide Drought Tracker (Abatzoglou et al., 2017)	0.4 (1.1)	Positive	Brooks (2004, 2005); Daszak et al. (2005); Davis et al. (2019); Leibowitz and Brooks (2007); Rodenhouse et al. (2009)
Average April area*	Pool attribute	m ²	NA	Pool inundation observation dataset	732 (2356.1)	Positive	Brooks (2005, 2009); Brooks and Hayashi (2002); Chandler et al. (2017); Leibowitz and Brooks (2007)
April area/depth ratio*	Pool attribute	Ratio	NA	Pool inundation observation dataset	1680.1 (3852.9)	Negative	Brooks (2005); Brooks and Hayashi (2002); Leibowitz and Brooks (2007)
Elevation*	Pool attribute	m	1/3 arc-second grid	1/3 arc-second digital elevation model (US Geological Survey, 2017)	237.9 (292.3)	Unknown ^d	Brooks (2005); Chandler et al. (2017); Leibowitz and Brooks (2007)
Latitude	Pool attribute	Decimal degrees	NA	Pool point locations from pool inundation observation dataset	42.1 (2.5)	Positive	Brooks (2005, 2009)
Coastal	Pool attribute	Binary	NA	Pool point locations; indicates whether pools were located <1 km from a coastline	NA	Positive ^e	McLaughlin et al. (2017)
Landforms	Landscape characteristic	Categorical	30-m grid	Landform on which pool is located (Theobald et al., 2015)	NA	Variable ^f	Calhoun et al. (2014); Rheinhardt and Hollands (2008)
Water-table depth (April–June minimum)*	Landscape characteristic	Cm below the soil surface	10-m grid	gSSURGO (Soil Survey Staff, 2016)	42 (45.5)	Negative	Brooks (2005); Calhoun et al. (2014); Leibowitz and Brooks (2007); Rheinhardt and Hollands (2008)
Soil hydrologic group (dominant condition)*	Landscape characteristic	Categorical	10-m grid	gSSURGO (Soil Survey Staff, 2016)	NA	Increase from A to D ^g	Brooks (2005); Calhoun et al. (2014); Leibowitz and Brooks (2007)

TABLE 1 (Continued)

Predictor ^a	Category	Units	Dataset type and resolution	Source	Mean (SD) ^b	Hypothesis ^c	References
Geologic permeability	Landscape characteristic	Log(k)	Polygons	Global Hydrogeology Maps (GLHYMPS) dataset (Gleeson et al., 2014)	-13.7 (1.8)	Positive ^b	Rheinhardt and Hollands (2008)
Geologic porosity	Landscape characteristic	Percentage	Polygons	GLHYMPS dataset (Gleeson et al., 2014)	0.1 (0.1)	Positive ^b	Rheinhardt and Hollands (2008)
Catchment impervious surface in 2011	Landscape characteristic	Percentage	Polygons	StreamCat dataset (Hill et al., 2016)	2.4 (6.1)	Unknown	Leibowitz and Brooks (2007)
Forest aboveground biomass in 2012*	Landscape characteristic	Kg/m ²	30-m grid	North Atlantic Landscape Conservation Cooperative (2014)	11.4 (5.2)	Negative ⁱ	Brooks (2009); Jones et al. (2018); Sun et al. (2000)
Landcover in 2011 ^{*j}	Landscape characteristic	Categorical	30-m grid	2011 National Land Cover Database (NLCD) (Yang et al., 2018)	NA	Variable	Babbitt et al. (2009); Calhoun et al. (2003); Grant (2005); Leibowitz and Brooks (2007); McLaughlin and Cohen (2013)
Reference evaporation (derived using Hargreaves 1985 method; Hargreaves & Allen, 2003)*	Climate	Mm	1-km grid	AdaptWest North American gridded climate dataset (AdaptWest Project, 2015)	848.2 (149.8)	Negative	Brooks (2004, 2009); Ray et al. (2016); Rodenhouse et al. (2009)
Growing-degree days (days above 5°C)	Climate	Degree-days	1-km grid	AdaptWest climate	848.2 (149.8)	Negative	Brooks (2009); Rodenhouse et al. (2009)
Annual heat-moisture index (ratio of mean annual temperature to mean annual precipitation)*	Climate	Ratio	1-km grid	AdaptWest climate	16.3 (3.1)	Negative	Brooks (2004, 2009); Daszak et al. (2005); Rodenhouse et al. (2009)
Precipitation as snow	Climate	Mm	1-km grid	AdaptWest climate	149.1 (109.5)	Positive, but varies by geography	Brooks (2009); Leibowitz and Brooks (2007); Rodenhouse et al. (2009)
Average summer (June to august) temperature	Climate	°C	1-km grid	AdaptWest climate	19.9 (2.5)	Negative	Brooks (2004, 2009); Rodenhouse et al. (2009)
Beginning of frost-free period	Climate	Julian date	1-km grid	AdaptWest climate	130.6 (12)	Positive	Brooks (2009); Rodenhouse et al. (2009)

^aOnly a subset of the candidate predictors in this table (marked with a *) were included in the final simplified models. For details on the model simplification procedures to produce more parsimonious final models, see supporting information sect. 3.

^bFor time-varying predictors, means and standard deviations (SD) were calculated across 3004 inundation observations used in pool inundation models. For all other predictors (pool attributes, landscape characteristics and climate variables), means and standard deviations were calculated across the 449 pools used in inundation models.

^cThe hypothesized relationship between each variable and vernal-pool inundation, for example, 'negative' for Julian day indicates that vernal-pool inundation decreases as Julian day increases from spring through summer. For landscape characteristics, the hypothesis refers to the relationship between the variable and pool hydroperiod, that is, likelihood of late-season inundation. References supporting hypotheses (provided in the References column) are drawn primarily from the literature on vernal pools of the northeastern United States, supplemented by studies of similar depression wetlands in other regions.

^dGroundwater contributions to pool inundation—but also losses to evapotranspiration—may be greater at lower elevations.

^eCoastal fog can suppress water losses from evapotranspiration.

^fHydrogeomorphic setting (e.g., pool location on slopes, flats, depressions and other landforms) influences pool hydroperiod through surface-runoff and groundwater dynamics.

^gSoil Group A indicates well-drained soils with lower runoff potential; Group D indicates poorly drained soils with higher runoff potential.

^hInundation in pools on more permeable geologic substrates tends to be maintained in part by groundwater rather than solely by precipitation.

ⁱGreater forest cover surrounding pools is expected to increase water losses by transpiration, however, greater canopy shading could reduce pool water losses from surface evaporation.

^jThe National Land Cover Database (NLCD) 'cultivated crops' and 'hay/pasture' categories were combined into a single category 'agriculture'. The 'shrub/scrub' and 'herbaceous' categories were combined into a single category 'grass/shrub'. Only those landcover categories representing at least five vernal pools were retained for modelling.

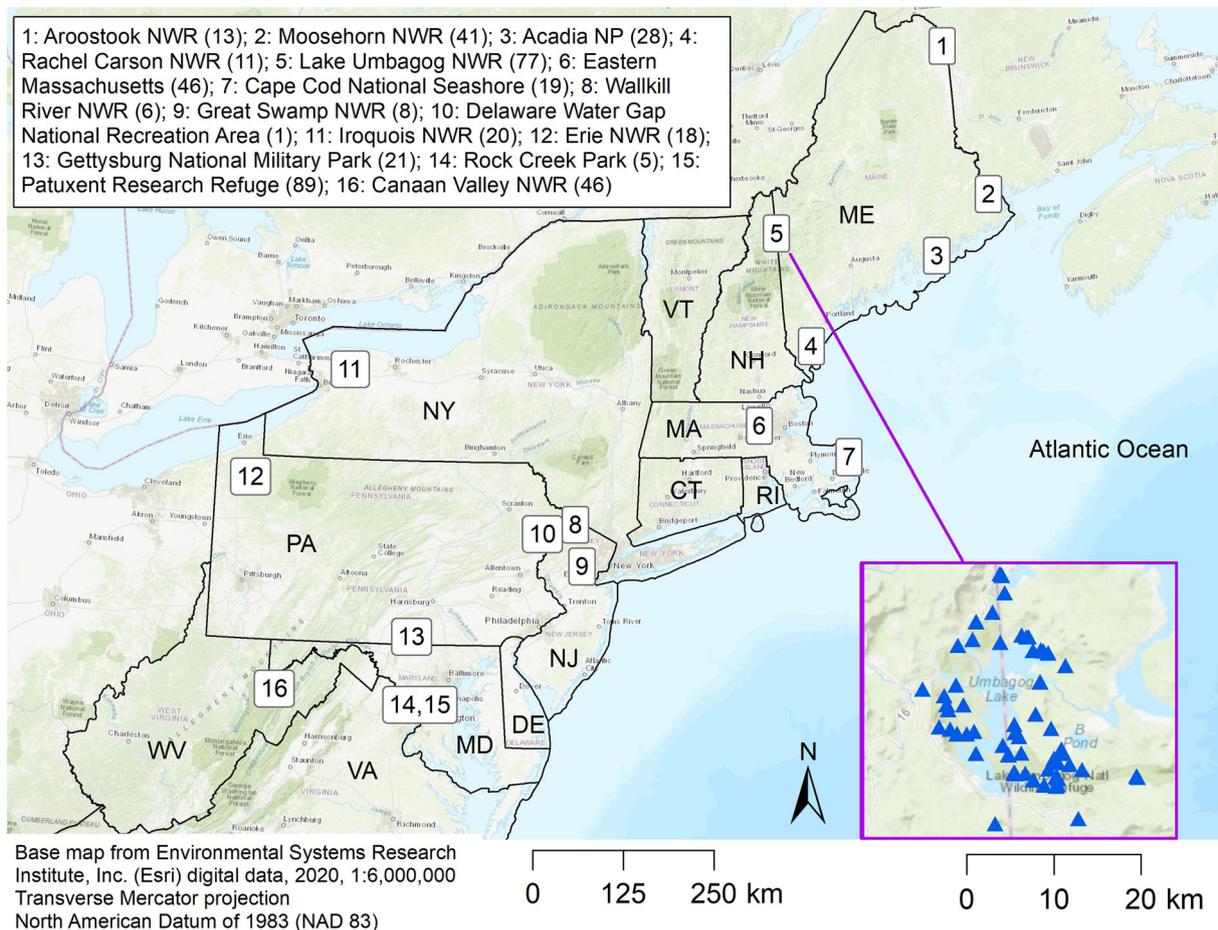


FIGURE 1 Vernal-pool locations across the northeastern United States. Map numbers correspond to unit names (e.g., protected areas) in the inset text box; numbers in parentheses indicate numbers of pools from each unit that were used in inundation models. NP, National Park; NWR, National Wildlife Refuge. WV, West Virginia, VA, Virginia, MD, Maryland, DE, Delaware, NJ, New Jersey, PA, Pennsylvania, NY, New York, CT, Connecticut, RI, Rhode Island, MA, Massachusetts, VT, Vermont, NH, New Hampshire, ME, Maine. Inset map in lower right shows vernal-pool locations at an example refuge, Lake Umbagog NWR

precipitation inputs (on the scale of days) in addition to longer-term weather indicators (on the scale of months or years) because variability in short-term precipitation accumulation has been shown to be an important driver of pool inundation patterns (Brooks, 2004). For short-term water inputs, cumulative antecedent precipitation was calculated as the sum of daily precipitation from the Parameter-elevation Regressions on Independent Slopes Model (PRISM; Daly et al., 1994) for a specified number of days (3, 5, 7 and 10) leading up to the day of each inundation observation. After performing a sensitivity analysis (Table S2), we chose 5-day cumulative antecedent precipitation to represent short-term water inputs. To represent medium-term water-balance conditions, Standardized Precipitation Evapotranspiration Index (SPEI) data were obtained from the WestWide Drought Tracker (Abatzoglou et al., 2017). SPEI is conceptually similar to the Standardized Precipitation Index (SPI) but also incorporates temperature-related effects on potential evapotranspiration (Vicente-Serrano et al., 2010). SPEI accounts for the difference between precipitation and potential evapotranspiration over varying time frames, normalized to local conditions. For example, for a June observation of pool

inundation, 3-month, 6-month, and 12-month SPEI represent precipitation and potential evapotranspiration from April–June, January–June, and May–June, respectively. We performed a sensitivity analysis using these SPEI time frames (Table S2) and selected 6-month SPEI to represent medium-term water-balance conditions. Finally, we represented long-term climatic drivers of pool inundation using 30-year (1981 to 2010) average climate variables from the AdaptWest Project (2015). Climate variables were selected for possible inclusion in pool-inundation models based on strength of correlation with observed pool inundation and plausible mechanistic relationships to drivers of pool inundation (i.e., relationships to the magnitude, form, and seasonal timing of precipitation and evapotranspiration; Table S1). We anticipated that pool inundation would be positively related to 5-day cumulative antecedent precipitation and SPEI, and negatively related to indices of aridity such as annual heat-moisture index (Table 1).

We also compiled landscape attributes (e.g., landcover and soil characteristics) that are known to influence local hydrology and pool-inundation patterns (Table 1; see hypotheses and references

therein). All dataset values were extracted directly to pool point locations, except for landcover type and forest aboveground biomass, which represent the upland areas surrounding pools. To assign values to pool locations for these datasets, we performed a sensitivity analysis using three possible buffer distances around pool point locations, with radii of 20, 50, and 100 m (Table S3). All data compilation was conducted in the R statistical language (R Core Team, 2017) using the packages *sp*, *raster*, *rgdal*, *mclust* and *rgeos*. Data and R processing scripts used in this study are available from Cartwright, Morelli, and Grant (2020).

2.4 | Inundation models

We represented vernal-pool inundation using four binary inundation metrics, H1 through H4, which represented presence or absence of inundated wetland habitat according to increasingly stringent thresholds of inundated depth and area. The H1 metric classified pools as inundated if any amount of water was observed, that is, inundated depth and area >0 . The H2, H3 and H4 metrics classified pools as inundated if they had inundated depth ≥ 5 cm and area ≥ 5 m², depth ≥ 10 cm and area ≥ 15 m², and depth ≥ 15 cm and area ≥ 25 m², respectively. For example, for all June observations in the dataset, roughly 73% would be classified as inundated according to the least-stringent definition (H1), compared to only 46% according to the most-stringent definition (H4).

We investigated potential drivers of pool inundation by constructing separate boosted regression tree (BRT) models for each of the four inundation metrics. BRT models are a class of machine-learning algorithm in which regression trees are fitted iteratively, with the primary trees explaining the largest deviation in the response variable (in this case, binary inundation metrics), with subsequent trees seeking to maximally explain the remaining error (i.e., to explain distribution in the residuals). Advantages of BRT models over other classification frameworks include their ability to capture complex interactions and non-linear relationships and their capacity to handle missing values and multiple predictor types, that is, continuous and categorical variables (De'ath, 2007; Elith et al., 2008; Hastie et al., 2001). All BRT models were constructed with Bernoulli error distribution, tree complexity (i.e., number of splits) = 5, bag fraction = 0.5, and 10-fold cross-validation. We used the *gbm.step* procedure in the R package *dismo* to systematically select the optimal learning rate and number of trees for each model so as to maximize the deviance explained and minimize overfitting, in each case ensuring >1000 trees for each model (Elith et al., 2008; Hijmans et al., 2016).

We evaluated BRT model performance using three statistics: (1) the percentage of deviance in the response variable (inundation metric) explained by the model, (2) the cross-validated correlation coefficient and (3) the mean area under the curve of the receiver-operator characteristic (ROC-AUC). ROC-AUC values can range from 0 to 1, representing the probability that a randomly selected positive inundation observation (pool was observed to be wet) has a higher predicted wetness probability than a randomly selected negative

observation (pool was observed dry). Thus, an ROC-AUC value of 0.5 would represent model performance no better than chance, and values increasing towards 1 indicate improved model ability to discriminate wet from dry inundation observations.

We constructed preliminary BRT models for the H1 through H4 inundation metrics using all candidate predictors in Table 1 ('full models'), a total of 22 predictors describing pool attributes, landscape characteristics, and weather and climate variables relevant to pool inundation patterns (see references in Table 1). We then conducted a three-step model simplification procedure to arrive at more parsimonious final models (Tables S4 through S6). The goal of model simplification was to remove predictors that were redundant and/or that could be removed without adversely affecting model predictive performance (Elith et al., 2008). Ten predictors were removed to produce simplified final models with 12 predictors. Model simplification did not substantially affect model performance (Table S6).

2.5 | Model predictions

BRT models for inundation metrics H1 through H4 were used to generate predictions of pool wetness under a variety of conditions. Predicted wetness probability was expressed as continuous probability values ranging from 0 to 1. To compare observed and predicted inundation for model accuracy calculations, a threshold of 0.6 was applied to these continuous probabilities to differentiate predictions of 'likely dry' from 'likely wet' pool inundation status, because this threshold maximized model prediction accuracy while approximately balancing type 1 and 2 error rates (Figure S1).

To test model prediction accuracy, we conducted leave-one-out cross-validation (LOOCV) by systematically withholding all observations from one pool at a time (as a test dataset) and generating predictions using all observations from all other pools (Tables S7 and S8). Thus, LOOCV accuracy statistics for each pool represent the effectiveness of the modelling approach in predicting that pool's inundation patterns using a model trained on all other pools in the dataset. Because pools varied in their LOOCV accuracy and in the numbers of observations per pool (from one to 17), we assigned pools to five categories of confidence in model predictions based on combined criteria for LOOCV accuracy and numbers of inundation observations. These confidence categories allow users of the prediction datasets to screen pools based on relative confidence in the accuracy of model predictions.

We created plots of predicted wetness probability on a daily time step from May 1 through July 31 for the 449 pools in the modelling dataset. Wetness predictions were generated under three weather scenarios: average conditions (SPEI = 0; 5-day cumulative precipitation = 10.8 mm, the median of observed cumulative precipitation values in the modelling dataset), dry conditions (SPEI = -1; cumulative precipitation = 0 mm), and wet conditions (SPEI = 1; cumulative precipitation = 26.0 mm, the 75th percentile of observed cumulative precipitation). Wetness predictions for each day under the three weather scenarios assumed the corresponding SPEI

value on that day and the corresponding cumulative precipitation for the five days leading up to that day (e.g., SPEI = 1 and a total of 26.0 mm of precipitation from June 1 to June 5 for a prediction on June 5 under the wet-conditions scenario). For each scenario, prediction curves for each pool were used to calculate inferred drying dates, that is, the Julian days at which the predicted wetness probability curves fell below the 0.6 threshold separating 'likely wet' from 'likely dry' status.

We then generated 300 sets of modelled wetness probability predictions for the pools in the dataset, using the four inundation definitions (H1 through H4), three weather scenarios (dry, average and wet), five climate scenarios (historical, and 2050s and 2080s under RCPs 4.5 and 8.5) and five time points: May 15, June 1, June 15, July 1 and July 15. The period May 15 through July 15 represents a critical period for pool-breeding amphibian life-cycle completion in this region (Brooks, 2004). The intent of providing multiple sets of wetness probability predictions was to enable managers and other stakeholders to choose the inundation definitions and time points of greatest relevance to their geographic location, species of interest and management priorities. For example, from the perspective of evaluating potential amphibian breeding habitat availability, identification of pools with a higher probability of having water available earlier in the season might be of interest, whereas for identifying possible refugia for amphibian life-cycle completion under future climate change, identification of pools holding water later in the season under future climate scenarios might be most important (Miller et al., 2018). These prediction datasets were then used to generate maps of predicted wetness probability under various combinations of inundation definitions, weather and climate scenarios, and time points, to enable identification of potential vernal-pool refugia according to a variety of possible refugia definitions.

3 | RESULTS

3.1 | Climate change projections for vernal pools

Across the protected areas ('units') containing vernal pools used for inundation modelling, climate models generally project warmer and drier summer conditions driven by increased evapotranspiration and longer growing seasons (Figure 2). Projected changes were generally greater under the RCP8.5 scenario than RCP4.5, with several variables showing pronounced changes by the 2080s under RCP8.5. Projected increases in annual heat-moisture index across units suggest that increasing mean-annual precipitation may be offset by increases in reference evaporation (closely linked to increasing summer mean temperatures), creating the potential for overall drier climatic conditions during the growing season. Across units, the frost-free period is projected to begin earlier, suggesting potential for earlier seasonal ramp-up of evapotranspiration if spring conditions become warmer and leaf-out timing shifts earlier. Meanwhile, snow-to-rain transitions (i.e., decreased fraction of precipitation falling as snow) suggest decreased early-spring snowpack. Longer and hotter growing seasons

(i.e., increases in growing-degree days and summer temperatures) suggest potential for increased summer drying of some vernal pools.

3.2 | Drivers of pool inundation

Of the 3004 observations (i.e., pool visits) in the dataset, 81% showed inundation at the time of observation according to the least-stringent inundation threshold for defining wetland inundation (H1), compared to 60% according to the most-stringent threshold (H4). As expected, pool inundation probability generally decreased from May through July. Partial-dependence plots from BRT models showed that—holding all other variables constant—the modelled likelihood of a pool being observed inundated (i.e., predicted wetness probability) declined from a maximum at the start of the modelled season (Julian Day 120, May 1) to a minimum at the end of the season (Julian Day 211, July 30; Figure 3a), which reflects that most of the pools in the study are seasonally (not permanently) inundated and thus are suitable habitat for vernal-pool-associated amphibians. Across the H1 through H4 models, Julian day was the most important or second-most important predictor based on relative influence values (Table 2).

Climate and weather patterns also influenced pool inundation probability. Both 5-day cumulative antecedent precipitation and 6-month SPEI had generally high relative influence values across models (Table 2), highlighting the importance of short- and medium-term meteorological conditions in driving pool inundation. Wetness probability increased in a generally linear fashion with increasing 5-day precipitation until approximately 40 mm, then levelled off at greater precipitation values (Figure 3b). Across the range of 6-month SPEI values between the 5th and 95th percentile of observed SPEI (dashed vertical lines in Figure 3), inundation likelihood was lowest for SPEI values near -1 (indicating moderate drought) and was greatest for SPEI values between 1 and 2 (indicating wetter-than-average conditions, Figure 3c). Predicted wetness probability generally declined with increasing 30-year average reference evaporation and annual heat-moisture index (Figure 3f,i), suggesting that inundation was more likely for pools in cooler, wetter climates after accounting for other variables in the models. The greater relative influence of 5-day precipitation and SPEI compared to 30-year climate variables (Table 2) suggests that shorter-term weather conditions were more important in explaining differences in pool inundation than long-term climate. Pool inundation did not show clear, unambiguous relationships to elevation (Figure 3g) and elevation had generally low relative influence across models (Table 2), suggesting that elevation was not a strong driver of pool inundation after accounting for weather and climate conditions.

Overall, the strongest predictor of inundation probability was average April inundated area (Table 2), with larger-area pools more likely to be inundated throughout the season (Figure 3d). Although average April area and April area-to-depth ratio were strongly positively correlated across pools (Spearman's $\rho = 0.89$), they showed opposite patterns in partial-dependence plots (Figure 3d,e). This finding suggests that, for pools of a given size at a given seasonal time point, pools with deeper, narrower geometry were more likely to be

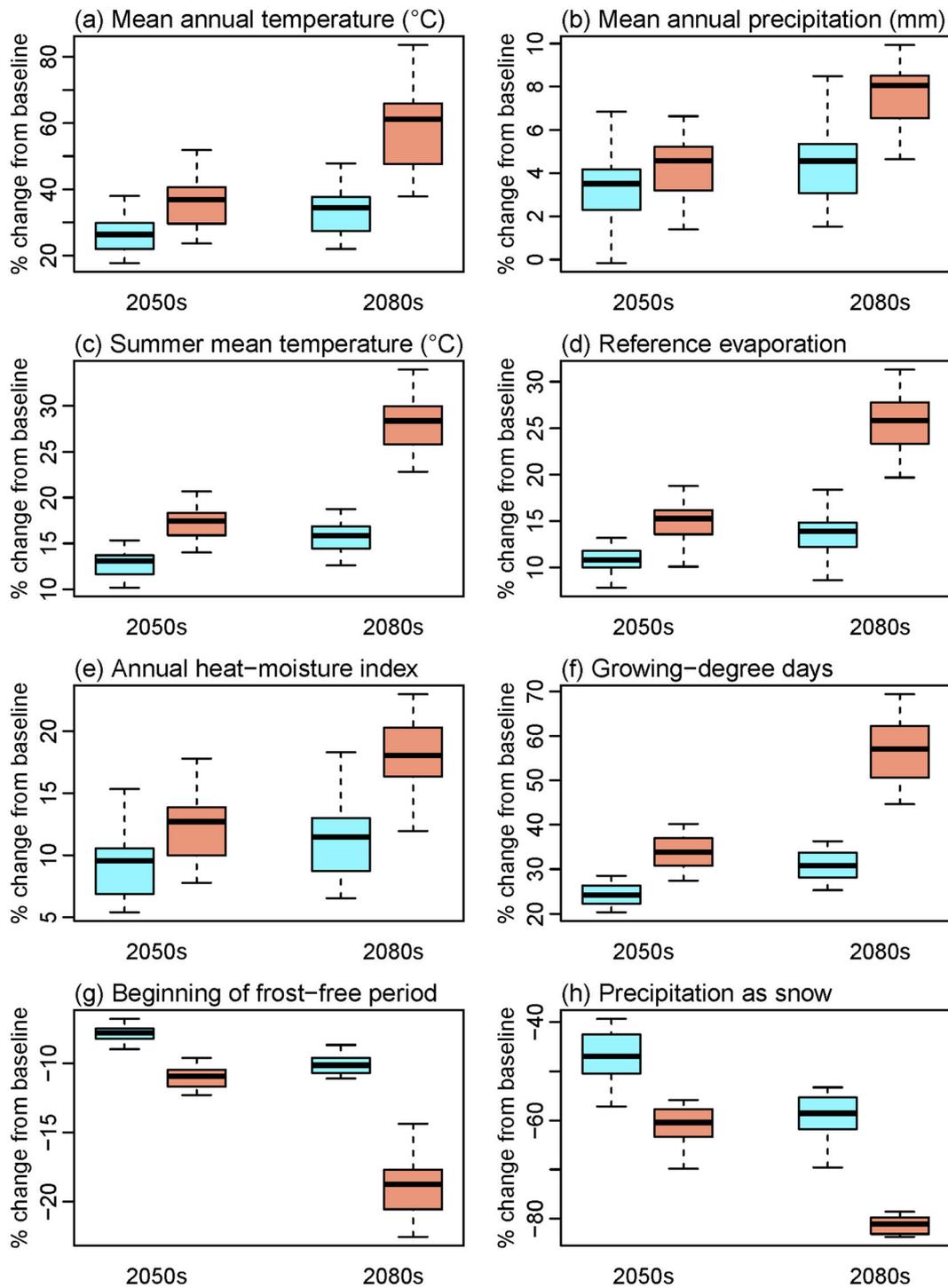


FIGURE 2 (a–h) Climate-change projections for the RCP4.5 and 8.5 emissions scenarios (blue and orange, respectively) for the 2050s (2041 through 2070) and 2080s (2071 through 2100), expressed as percentage change relative to a baseline historical period (1981 through 2010). Boxplots represent variability across the protected areas (‘units’) containing pools used in inundation models. Projections represent ensembles averaged from 15 climate models (AdaptWest project, 2015; Wang et al., 2016)

inundated than pools with broader, shallower geometry, possibly related to the role of surface evaporation in pool drying.

Several landscape characteristics also helped explain pool inundation patterns, although landscape characteristics were generally less influential than pool surface area, seasonal timing (i.e., Julian day),

and recent precipitation (Table 2). Predicted wetness probability showed moderate declines with increasing forest aboveground biomass in a 50-m radius around pools (Figure 3h). Wetness probability was generally lowest for pools in predominantly agricultural areas and highest for pools surrounded by herbaceous wetlands (Figure 3j).

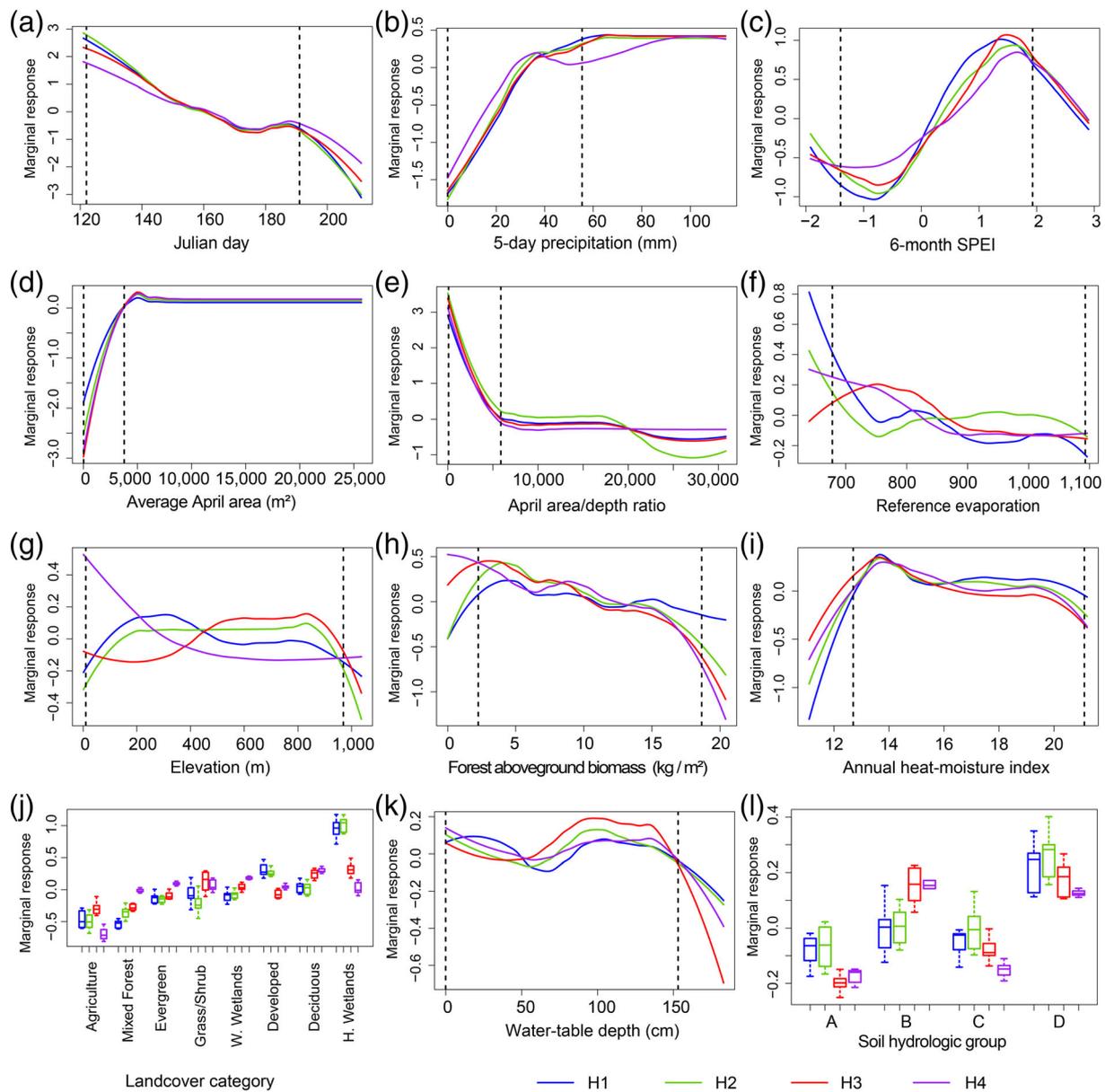


FIGURE 3 (a–l) Partial-dependence plots from simplified boosted regression tree models, relating likelihood of vernal-pool inundation (vertical axes) with timing, climate, pool and landscape characteristics (Table 1). Coloured lines represent loess-smoothed averages across 10 iterations per model. To reduce the influence of outliers, interpretation of relationships is focused on the region of each plot between the dashed vertical lines, representing 5th and 95th percentiles of the predictors. H1 through H4 inundation metrics are binary representations of pool inundation defined by the following thresholds: H1, inundated depth and area >0; H2, inundated depth ≥ 5 cm and area ≥ 5 m²; H3, inundated depth ≥ 10 cm and area ≥ 15 m²; H4, inundated depth ≥ 15 cm and area ≥ 25 m². 6-month SPEI is standardized precipitation evapotranspiration index calculated using 6-month antecedent conditions. In plot j, landcover categories Evergreen, W. wetlands, developed, deciduous, and H. wetlands represent evergreen forest, woody wetlands, developed open space, deciduous forest, and herbaceous wetlands, respectively

Little difference in inundation likelihood was apparent between pools surrounded by deciduous versus evergreen forest. The influence of water-table depth (minimum from April to June) was low across models (Table 2) and did not show clear relationships to pool inundation (Figure 3k). Although relative influence of soil hydrologic group was also low, pools located on well-drained soils (Group A) had the lowest predicted wetness probability whereas pools on poorly-

drained soils (Group D) had the highest probability (Figure 3l), suggesting that vernal-pool inundation may have been supported by soil types with high runoff potential and poor drainage. Several other landscape characteristics—including landform type, catchment impervious surface, geologic permeability and porosity, and coastal location—showed such minimal influence in preliminary models that they were dropped by the model simplification procedure (Table S4).

TABLE 2 Model performance statistics and relative influence values for simplified boosted-regression tree (BRT) models of vernal-pool inundation

	H1	H2	H3	H4
Number of trees	3000–4000	3000–4000	3000–4000	2500–3000
Cross-validated correlation	0.72 (0.0063)	0.74 (0.0042)	0.75 (0.0057)	0.75 (0.0032)
Percentage deviance explained	0.77 (0.0169)	0.76 (0.0156)	0.75 (0.0184)	0.70 (0.0084)
ROC-AUC	0.93 (0.0032)	0.93 (0)	0.93 (0.0032)	0.93 (0.0042)
Relative influence values				
	H1	H2	H3	H4
Average April area	13.57 (0.26)	17.47 (0.36)	23.57 (0.48)	29.61 (0.46)
Julian day	16.67 (0.24)	17.0 (0.31)	13.37 (0.23)	11.03 (0.26)
5-day precipitation	12.42 (0.19)	11.36 (0.2)	10.03 (0.23)	8.29 (0.15)
6-month SPEI	11.38 (0.21)	10.29 (0.21)	9.8 (0.16)	7.89 (0.17)
April area/depth ratio	9.1 (0.15)	8.48 (0.16)	8.64 (0.11)	9.16 (0.25)
Reference evaporation	9.22 (0.21)	7.62 (0.21)	8.37 (0.26)	8.35 (0.23)
Forest aboveground biomass	6.6 (0.19)	6.71 (0.17)	6.85 (0.12)	5.78 (0.15)
Annual heat-moisture index	6.19 (0.3)	5.68 (0.22)	5.63 (0.18)	5.06 (0.17)
Elevation	5.16 (0.12)	5.28 (0.19)	4.52 (0.1)	5.74 (0.18)
Landcover category	4.36 (0.17)	4.75 (0.17)	4.36 (0.15)	4.3 (0.14)
Water-table depth	3.46 (0.09)	3.25 (0.13)	3.09 (0.11)	2.87 (0.11)
Soil hydrologic group	1.86 (0.11)	2.1 (0.13)	1.78 (0.09)	1.95 (0.08)

Note: Values are presented as means (standard deviations in parentheses) across 10 iterations for each model. H1 through H4 inundation metrics are binary representations of inundation defined by the following thresholds: H1, inundated depth and area >0; H2, inundated depth ≥ 5 cm and area ≥ 5 m²; H3, inundated depth ≥ 10 cm and area ≥ 15 m²; H4, inundated depth ≥ 15 cm and area ≥ 25 m². For each inundation metric, the top 3 predictors with greatest mean relative influence are bolded. 6-month SPEI is standardized precipitation evapotranspiration index calculated using 6-month antecedent conditions. ROC-AUC is the mean area under the curve of the receiver-operator characteristic. All models were constructed with a learning rate of 0.015.

3.3 | Predictions of pool wetness

Pool-specific model prediction accuracy based on LOOCV (i.e., the percentage of a given pool's inundation observations that were modelled correctly using a model trained on all other pools) ranged from 0% to 100%, with mean prediction accuracy ranging from approximately 80% to 87% and median prediction accuracy ranging from 90% to 100% across the H1 through H4 models (Tables S7 and S8). Using combined criteria of LOOCV prediction accuracy and number of observations per pool, approximately 54% of pools were assigned confidence of 'moderate' or better, 42% had confidence of 'moderately high' or better, and 13% had 'very high' confidence in model predictions (Table 3).

Pools demonstrated a variety of modelled seasonal dry-down patterns in response to short-term weather and future climate scenarios. Pools were generally predicted to desiccate earlier under the dry weather scenario and later under the wet weather scenario, although responses of modelled pool drying to weather and climate scenarios varied substantially across pools (examples in Figure 4). Under historical climate conditions, the example pool in Figure 4a was predicted to dry in late May in dry weather, in early July in average weather, and in late July in wet weather. Using projected climate conditions for the 2080s under RCP 8.5, this pool was projected to become dry slightly earlier under dry conditions and roughly 2 weeks earlier under

average conditions, with no change in inferred drying date under wet conditions. Some pools, especially in the dry weather scenario, were predicted to be dry during the entire seasonal modelling period. For example, under both historical and future climate scenarios, the pool in Figure 4b was predicted to be dry (wetness probability <0.6) from May 1 through July 15 under the dry and average weather scenarios and was predicted to dry in late May under the wet weather scenario. By contrast, other pools (e.g., Figure 4c) were predicted to be inundated (wetness probability >0.6) during the entire seasonal modelling period. Under both historical and future climate conditions, this pool was projected to remain inundated past July 15 under all weather scenarios.

Distributions of predicted wetness probability across pools varied according to inundation definition, weather scenario, Julian date and climate scenario (Figure 5). For example, among pools with 'moderately high' or 'very high' prediction confidence, under the H2 inundation definition on May 15 in the average weather scenario under historical climate conditions (Figure 5a), the median and 25th percentile of predicted wetness probability were 0.95 and 0.68, respectively, compared to 0.80 and 0.25, respectively, under the more stringent H4 definition (Figure 5c). Predicted pool wetness probabilities were generally lower using future climate projections compared to historical climate variables. For example, for pools with 'moderately high' or 'very high' prediction confidence, median wetness probability for the H2

TABLE 3 Confidence categories for model predictions based on cross-validation accuracy and numbers of inundation observations

Category of confidence in model predictions	Criteria ^a	Number of pools ^b	Percentage of pools ^b	Cumulative percentage of pools ^c
Very high	≥10 observations and ≥90% accuracy	58	12.9	12.9
Moderately high	≥5 observations and ≥80% accuracy	133	29.6	42.5
Moderate	≥5 observations and ≥70% accuracy	53	11.8	54.3
Moderately low	≥3 observations and ≥60% accuracy	80	17.8	72.2
Very low	<3 observations or <60% accuracy	125	27.8	100
Total		449	100	

^aNumbers of observations in the stated criteria refer to the number of inundation observations for each pool (which ranged from 1 to 17); accuracy refers to pool-specific accuracy calculated based on leave-one-out cross-validation (supporting information sect. 5), with accuracy having been averaged for each pool across the H1 through H4 inundation metrics.

^bNumbers of pools and percentages of pools for each confidence category represent the pools meeting the stated criteria minus the pools having a higher category of confidence.

^cFor each confidence category, the cumulative percentage of pools represents the percentage of pools having that level of confidence or greater.

metric on June 1 under dry weather conditions was 0.65 under historical climate (Figure 5a) and dropped to 0.36 in the 2080s under RCP 8.5 (Figure 5b). For a given combination of inundation definition, weather and climate scenario, overall likelihood of pool wetness generally decreased from May 15 through July 15. Pool wetness probability increased with increasingly wet weather conditions for all inundation definitions, climate scenarios and Julian dates.

3.4 | Potential vernal-pool refugia

Maps of predicted wetness probability—stratified by inundation metric, seasonal time point, and weather and climate scenarios—can be used to identify pools with the greatest likelihood of remaining inundated under a variety of conditions. Examples for the Patuxent Research Refuge in Maryland (Figure 6) show subsets of pools with predicted wetness probability >0.6 (in blue) under the dry weather scenario for two seasonal time points and two climate scenarios. Such maps can highlight subsets of pools that are projected to remain inundated under adverse weather conditions (i.e., the dry weather scenario), late-season time points (e.g., July 1 or July 15), and/or future climate projections. Through an online interactive web application (Cartwright, 2020), users can specify the inundation metric, seasonal time point, and weather and climate scenarios of interest to explore multiple options for defining and identifying refugial vernal pools, for example, depending on geographic location and species of interest.

Modelled pool-drying curves (Figure 4), distributions of predicted pool wetness (Figure 5), and maps of predicted pool wetness probability (examples in Figure 6) can be combined to identify potential vernal-pool refugia according to inundation thresholds and dates of interest. For example, predicted pool wetness distributions (Figure 5) suggest that relatively few pools across the northeastern

United States will be inundated (according to either the H2 or H4 definitions) through early-to-mid July in the dry weather scenario, and that this scarcity of late-season pool inundation will be exacerbated under climate change (i.e., by the 2080s under the RCP 8.5). However, some pools show relatively high late-season predicted wetness probability even under dry weather and future climate scenarios (example in Figure 4C), suggesting their potential as hydrologic refugia from droughts and climate change.

If we define vernal-pool refugia as pools with ≥60% probability of holding any amount of water (H1 definition) by July 1 under dry weather and historical climate conditions (Table 4), then modelling results identify 168 refugial pools across all refuge units (37% of 449 pools). Of these, 111 pools have prediction confidence of ‘moderate’ or better. Seventy-one pools (16%) retain ≥60% July 1 dry-weather wetness probability by the 2080s under RCP 8.5, of which 60 pools have prediction confidence of ‘moderate’ or better. While pools meeting this definition of refugia were distributed across most units, prevalence of refugial pools was uneven across units and was generally highest for units in Maine, that is, Acadia National Park and Aroostook, Moosehorn, and Rachel Carson National Wildlife Refuges. Numbers and percentages of pools meeting this refugia definition were generally lower for predictions using climate conditions for the 2080s under RCP 8.5 compared to those using historical climate conditions; however, several units were still projected to have some pools meeting this refugia definition under climate change. We stress that this definition of refugia represents only one of multiple possible definitions. For example, while all results in Table 4 rely on July 1 predictions, different seasonal time points for refugia identification might be appropriate for different geographic areas, species of interest or management applications (Paton & Crouch, 2002).

Average April inundated area was a strong predictor of observed inundation patterns (Table 2), with larger-area pools having more

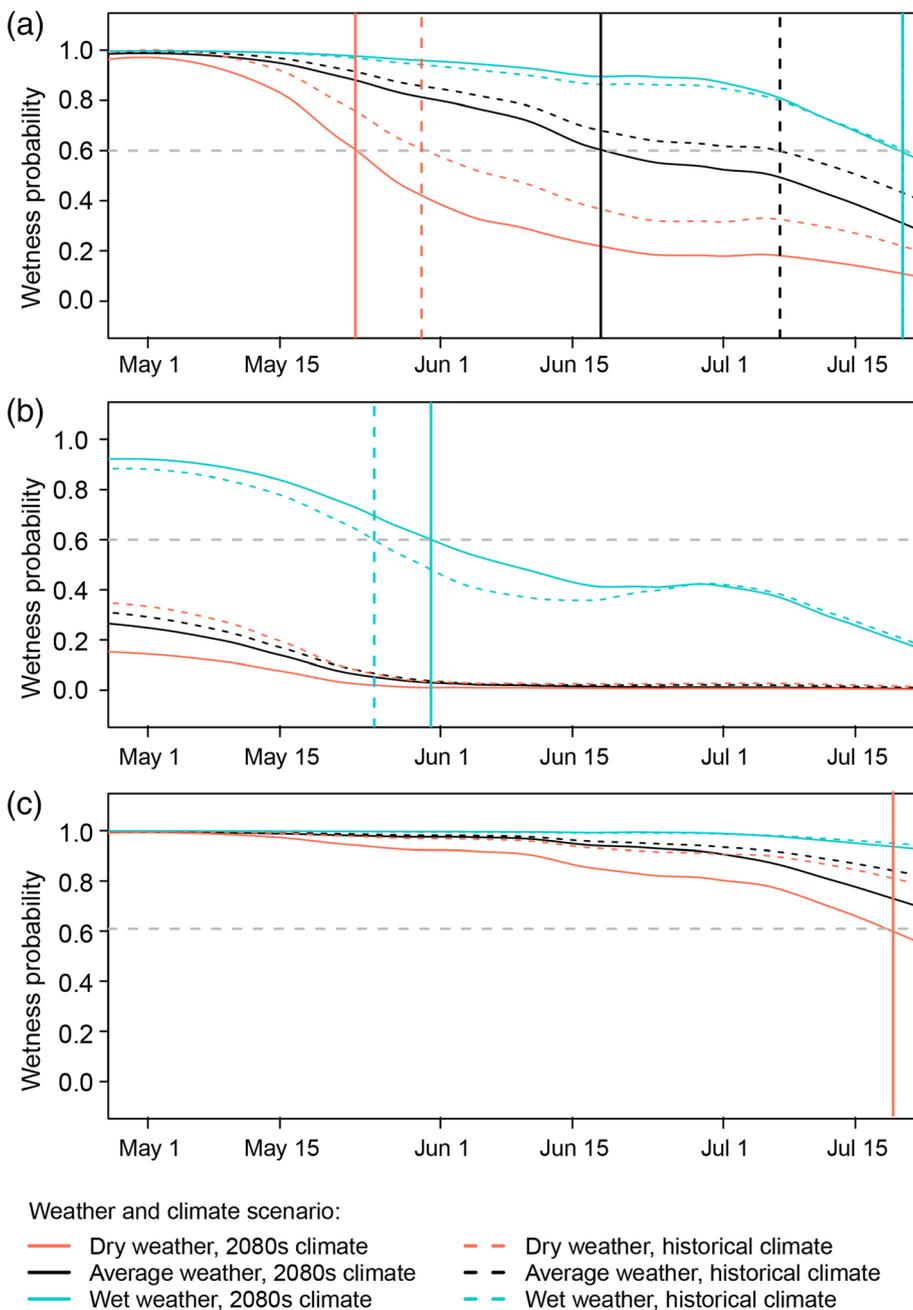


FIGURE 4 Examples of modelled wetness predictions for three pools showing (a) varying responses of inundation across weather and climate scenarios, as well as pools with (b) generally low and (c) generally high levels of predicted wetness probability. Curves depict loess-smoothed model predictions of wetness probability (averaged across 10 model iterations), for the dry, average and wet weather scenarios using the H2 inundation definition, using models with historical climate (dashed lines) and projected climate in the 2080s under representative concentration pathway 8.5 (solid lines). Pools were predicted to be 'likely dry' once their wetness probabilities fell below 0.6, corresponding to inferred drying days depicted as vertical lines. These example pools had cross-validation accuracy of (a) 93%, (b) 96% and (c) 100%

frequent inundation than smaller-area pools (Figure 3). This relationship was reflected in predicted wetness probability values, which were positively correlated with pool area across inundation metrics, prediction dates, and weather and climate scenarios (Tables S9 through S12). Thus, larger pools tended to have greater predicted wetness probability and might be more likely to serve as hydrologic refugia than smaller pools under a range of weather and climate conditions.

4 | DISCUSSION

In this study, pool-inundation models successfully represented inundation patterns for several hundred vernal pools at a regional scale,

using information on a variety of landscape and pool-specific attributes in conjunction with seasonal timing and climate variables. While relationships of some of these predictors to pool inundation were well understood from previous investigations (e.g., antecedent precipitation) others have been less well studied (e.g., forest biomass surrounding pools; Table 1). A machine-learning approach enabled us to evaluate >20 such potential influences on inundation, including categorical variables, while ultimately drawing conclusions from more parsimonious, simplified models (Table 1). In contrast to previous studies that examined hydrologic dynamics in only one or a handful of pools at the site scale (e.g., Brooks, 2000, 2004; Dodd, 1994; Greenberg et al., 2015) or for only a small number of years (e.g., Babbitt et al., 2003, 2009; Baldwin et al., 2006; Brooks, 2000; Brooks &

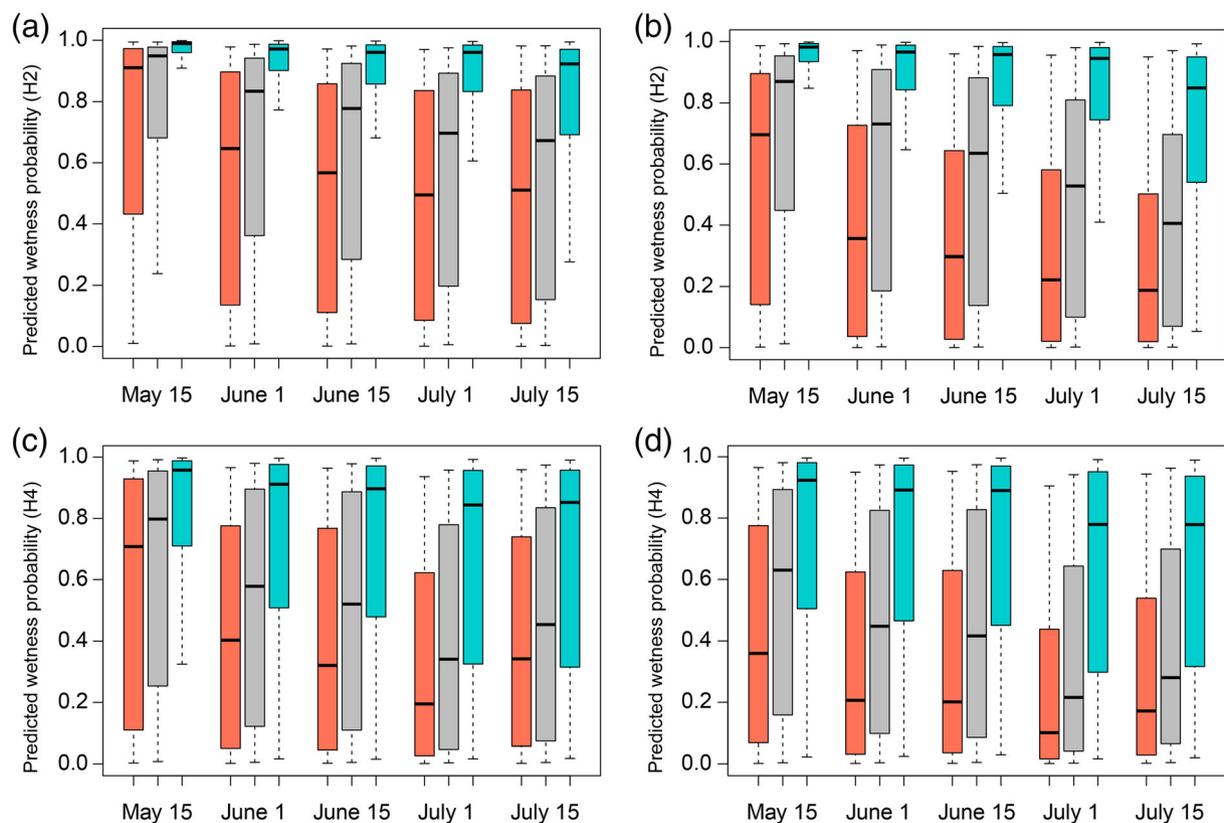


FIGURE 5 Distributions of predicted wetness probability of vernal pools in the modelling dataset for (a and b) the H2 inundation metric and (c and d) the H4 inundation metric, using model outputs with (a and c) historical climate variables and (b and d) climate projections for the 2080s under RCP 8.5. Dry, average and wet weather conditions are represented in orange, grey and blue, respectively. Because H4 is a more stringent metric than H2 for classifying pools as inundated, distributions of predicted wetness probability for H4 (c and d) are generally lower than for H2 (a and b). Distributions represent only the subset of pools with ‘moderately high’ or ‘very high’ prediction confidence

Hayashi, 2002; Chandler et al., 2017), this study incorporated roughly 3000 observations from 449 pools across the northeastern United States, collected under a variety of climate conditions over a 13-year period. By simulating seasonal dry-down curves (i.e., declining likelihood of inundation from late spring into summer) for individual pools under various climate and weather scenarios, models from this study could be used to identify pools from among the sampled set that might be most likely to remain inundated later into the summer under droughts and future climate conditions. Such models provide a potentially powerful tool to investigate climate effects on pool hydrologic regimes and to identify pools that might function as hydrologic refugia.

In vernal pools and related seasonal wetland ecosystems, hydrologic regimes are of primary importance in determining habitat quality for amphibians. Hydroperiod influences wetland geochemistry, water quality, litter decomposition, carbon cycling, invertebrate community composition and food webs (Babbitt et al., 2003; Boven et al., 2008; Brooks, 2000; Cartwright & Wolfe, 2016; Chandler et al., 2016; Golladay et al., 1997). Potential exists for earlier and/or more rapid pool drying—for example, from drought intensification and increased evapotranspiration under climate change—to interfere with reproductive success and long-term population viability for a number of

amphibian species of conservation concern (Brooks, 2009; Chandler et al., 2016; Daszak et al., 2005; Greenberg et al., 2015; Ray et al., 2016; Walls et al., 2013). These species generally function as habitat specialists, and many have larval growth and development periods that are adapted to historical ranges of timing for pool dry-down (Babbitt et al., 2003; Baldwin et al., 2006; Brooks, 2004; Seigel et al., 2006). While timing of metamorphosis is a plastic trait for many temporary-wetland-associated species, minimum hydroperiods are necessary for successful recruitment and faster metamorphosis may induce a lifetime fitness cost (Amburgey et al., 2016; Cabrera-Guzmán et al., 2013; Semlitsch et al., 1988). As a result, shifts in seasonal timing of pool filling and drying of even a few weeks can affect populations of temporary wetland-breeding amphibian species (Baldwin et al., 2006; Calhoun et al., 2014; Seigel et al., 2006).

While there are a number of putative causes of amphibian population declines, droughts and associated early pool-drying events have been linked to catastrophic reproductive failure, population crashes and local extirpations of pool-breeding amphibians (Palis et al., 2006; Richter et al., 2003; Scheele et al., 2012; Seigel et al., 2006; Semlitsch, 1987; Taylor et al., 2006). Many pool-breeding amphibian species exhibit high levels of interannual variability in reproductive success and have evolved to cope with

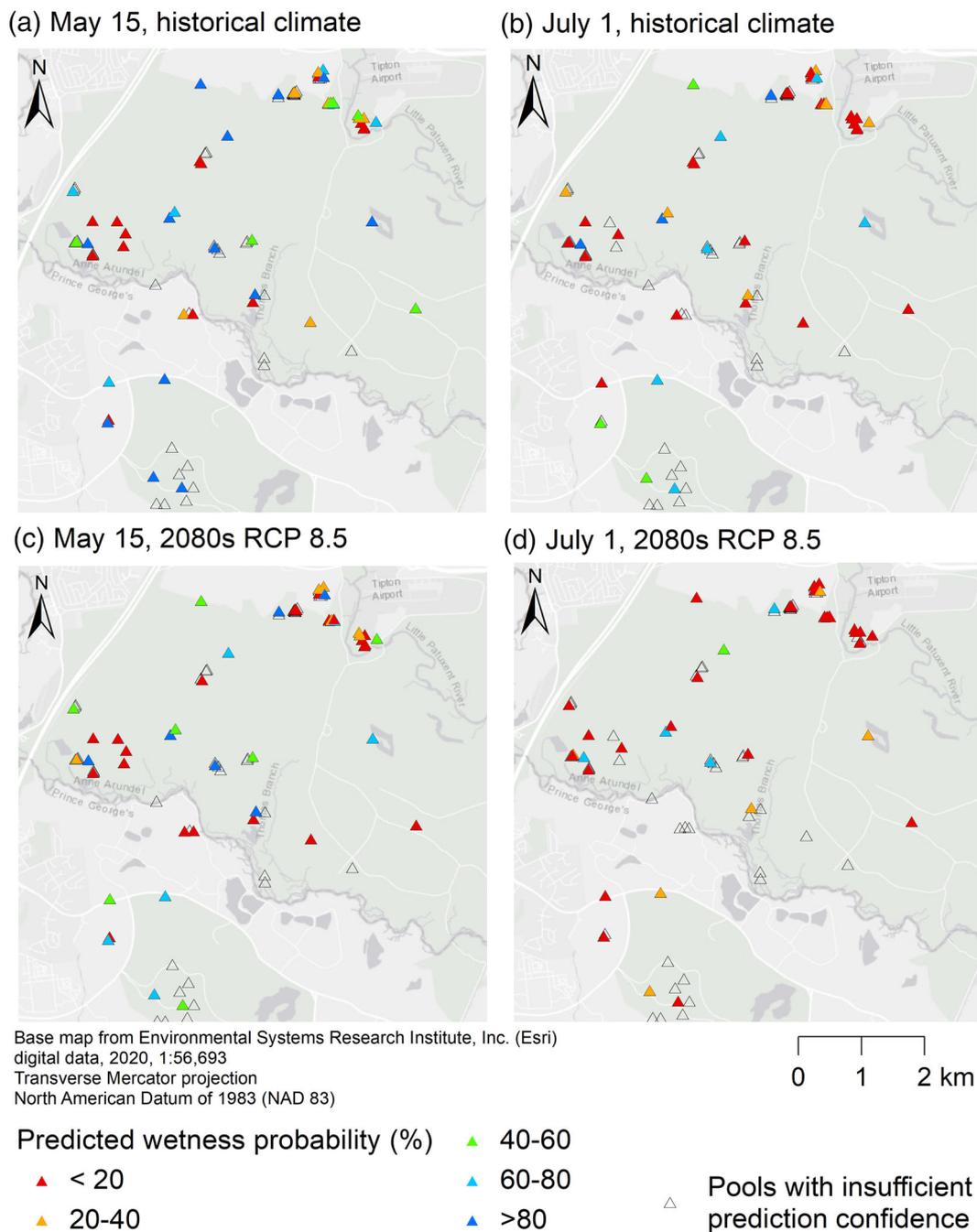


FIGURE 6 Maps of predicted wetness probability for vernal pools at the Patuxent research refuge in Maryland, USA, depicting likelihood of inundation on (a and c) May 15 and (b and d) July 1, using (a and b) historical climate variables and (c and d) projected climate variables for the 2080s under RCP 8.5. All predictions are for the H1 inundation metric and the dry weather scenario. These are four examples of 300 sets of wetness probability predictions generated under various inundation definitions, seasonal time points, and weather and climate scenarios. Predictions are displayed only for pools categorized as having ‘moderately high’ or ‘very high’ prediction confidence based on cross-validation accuracy and numbers of observations; all other pools are displayed as hollow triangles. In (d), blue triangles (i.e., pools with $\geq 60\%$ predicted wetness probability) could indicate hydrologic refugia

stochastic years of reproductive failure (Brooks, 2004; Semlitsch et al., 1996; Taylor et al., 2006). Although periodic reproductive failure may not result in metapopulation-level declines, increases in the frequency of years with reproductive failure could harm long-term population viability (Brooks, 2004; Daszak et al., 2005; Taylor et al., 2006).

In this context, effective management of vernal pools and the amphibian populations they support requires the ability to anticipate potential hydrologic changes, which in turn requires understanding of the interacting factors that shape vernal-pool hydrologic regimes. Findings from this study confirm that vernal-pool hydrology is influenced by a complex array of drivers, ranging in scale from regional

TABLE 4 Numbers and percentages of pools across units (protected areas) meeting one possible definition of refugia ($\geq 60\%$ predicted probability of holding any amount of water on July 1 under dry weather conditions)

Unit name	Number of pools	Historical climate		2080s, RCP 8.5	
		Refugia: All pools	Refugia: Confidence filter	Refugia: All pools	Refugia: Confidence filter
Acadia NP	28 (21)	22 (78.6%)	17 (81%)	14 (50%)	13 (61.9%)
Aroostook NWR	13 (9)	11 (84.6%)	9 (100%)	0 (0%)	0 (0%)
Eastern Massachusetts NWR	46 (27)	16 (34.8%)	12 (44.4%)	1 (2.2%)	1 (3.7%)
Cape cod National Seashore	19 (0)	6 (31.6%)	Na	1 (5.3%)	Na
Canaan Valley NWR	1 (0)	0 (0%)	Na	0 (0%)	Na
Delaware water gap NRA	46 (28)	17 (37%)	14 (50%)	15 (32.6%)	13 (46.4%)
Erie NWR	18 (11)	4 (22.2%)	3 (27.3%)	3 (16.7%)	3 (27.3%)
Gettysburg NMP	21 (0)	1 (4.8%)	Na	0 (0%)	Na
Great swamp NWR	8 (0)	1 (12.5%)	Na	0 (0%)	Na
Iroquois NWR	20 (16)	5 (25%)	5 (31.2%)	7 (35%)	6 (37.5%)
Lake Umbagog NWR	77 (37)	31 (40.3%)	19 (51.4%)	14 (18.2%)	8 (21.6%)
Moosehorn NWR	41 (18)	33 (80.5%)	13 (72.2%)	7 (17.1%)	7 (38.9%)
Patuxent research refuge	89 (66)	13 (14.6%)	12 (18.2%)	3 (3.4%)	3 (4.5%)
Rachel Carson NWR	11 (11)	7 (63.6%)	7 (63.6%)	6 (54.5%)	6 (54.5%)
Rock Creek park	5 (0)	0 (0%)	Na	0 (0%)	Na
Wallkill River NWR	6 (0)	1 (16.7%)	Na	0 (0%)	Na
All units	449 (244)	168 (37.4%)	111 (45.5%)	71 (15.8%)	60 (24.6%)

Note: (1.) In the 'number of pools column', the first number denotes all pools; the number in parentheses is the number of pools having prediction confidence of 'moderate' or better. (2.) All results in the 'refugia' columns were calculated according to one possible definition of refugia, that is, $\geq 60\%$ predicted probability of holding any amount of water (H1) on July 1 under dry weather conditions. Numbers of pools meeting the definition are listed, followed by percentages of pools (in parentheses). These results show only one possible approach to defining refugia, whereas other definitions using other inundation metrics, seasonal time points, and weather conditions could also be proposed. (3.) Results in the 'refugia (confidence filter)' columns represent only those pools for each unit having prediction confidence of 'moderate' or better; confidence categories are defined in Table 3. Abbreviations: NMP, National Military Park; NP, National Park; NRA, National Recreation Area, NWR, National Wildlife Refuge.

to site-specific (Brooks, 2004, 2005; Brooks & Hayashi, 2002; Calhoun et al., 2014; Grant, 2005; Leibowitz & Brooks, 2007). Pool-inundation models in this study successfully represented known seasonal dry-down patterns (Brooks, 2004, 2005), with inundation likelihood decreasing from early May to late July (Figures 3 and 4). Seasonality was represented by Julian day in models, which serves as a proxy for accumulated water losses from evapotranspiration. Julian day was not strongly correlated with other model predictors (Table S5) including recent precipitation, in agreement with the assessment by Brooks (2004, 2005) that vernal-pool inundation seasonality is largely driven by seasonality of evapotranspiration rather than precipitation. As expected, dry-down curves varied substantially among pools (e.g., Figure 4). Relative-influence values (Table 2) suggested strong roles of precipitation and evapotranspiration over relatively short (daily-to-monthly) time scales in shaping pool hydrology, in agreement with previous studies (Brooks, 2004; Davis et al., 2019; Greenberg et al., 2015). This importance of weather conditions was notable in the modelled dry-down curves for many pools under dry conditions relative to wet or average conditions (examples in Figure 4) and in distributions of inundation probability under

various weather scenarios (Figure 5). Overall, this study lends credence to concerns that vernal-pool hydrology may be sensitive to droughts and, consequently, that habitat for pool-breeding amphibians could be vulnerable to drought intensification and stronger evaporative demand under climate change (Brooks, 2004, 2009; Greenberg et al., 2015; Leibowitz & Brooks, 2007; Ray et al., 2016; Rodenhouse et al., 2009; Scheele et al., 2012).

Differences among vernal pools in their hydrologic regimes and their responses to weather and climate drivers can be linked to a variety of pool-specific attributes. We found that larger and deeper pools may be more likely to remain inundated later into the summer, consistent with our hypothesis (Table 1) and with previous studies and expectations based on the physical dynamics of surface evaporation (Brooks, 2005; Brooks & Hayashi, 2002; Leibowitz & Brooks, 2007; Chandler et al., 2017; but see Snodgrass et al., 2000). Future modelling efforts could benefit from more detailed data on pool-basin bathymetry, such as from Lidar or field surveys (Brooks & Hayashi, 2002; Faccio et al., 2016), to enable more precise evaluation of relationships between pool hydrologic dynamics and pool-basin area, depth, and morphology. Site-scale data on soil and stratigraphy

would also be very useful, including measurements of physical characteristics of pool-basin substrates (e.g., particle size, organic matter and drainage characteristics). Lacking such site-scale data at the regional scale of this study, we relied on soil-survey information (Soil Survey Staff, 2016). Our finding of greater predicted wetness probability for pools on poorly-drained than well-drained soil types reflects the general understanding of relationships between pool inundation dynamics and soil permeability and hydraulic conductivity (Grant, 2005; Leibowitz & Brooks, 2007; Rheinhardt & Hollands, 2008). For regional-scale studies in which substrate sampling is impractical across large numbers of vernal pools, soil-survey information may allow for valuable inferences. However, we acknowledge that fine-scale heterogeneity in pool substrate characteristics may be hydrologically important yet poorly represented by soil-survey information (Calhoun et al., 2014; Rheinhardt & Hollands, 2008), which may help explain the generally low relative-influence values for the soil-survey attributes representing water-table depth and soil hydrologic group (Table 2). Similarly, further investigation of potential groundwater interactions in vernal pools would benefit from site-level hydrogeologic data collection (e.g., installation of monitoring wells and piezometers; Barton et al., 2008; Chandler et al., 2017; O'Driscoll & Parizek, 2003). In some cases, groundwater influences can be inferred from water chemistry (i.e., specific conductance) and pool substrate characteristics (Brooks, 2005; Calhoun et al., 2014).

Pool substrate characteristics and degree and type of groundwater interactions are commonly a product of a pool's topographic position and geomorphic setting in the larger landscape (Rheinhardt & Hollands, 2008). In preliminary models, we represented landscape position using 30-m landform categories (i.e., pool was located on a ridge, upper slope, lower slope, or valley), but this attribute was removed from final models through the model simplification procedure (Table S4). Instead, landscape setting may have been partially captured by the surrounding landcover attribute, for example, greater inundation likelihood in pools surrounded by herbaceous wetlands relative to more upland landcover types (Figure 3).

Models in this study indicated that pool inundation may vary slightly depending on surrounding landcover and decrease somewhat with increasing forest biomass in the uplands immediately surrounding pools, in agreement with other studies linking upland land-use to wetland hydrology and habitat (Table 1; Babbitt et al., 2009; Jones et al., 2018; McLaughlin & Cohen, 2013; Sun et al., 2000). Site-scale information on vegetation type, canopy cover and forest transpiration rates could help refine relationships between upland vegetation and pool-inundation patterns. We note that even if upland forest biomass negatively affects late-season probability of pool inundation—perhaps because of demand from forest transpiration on soil water reserves in the vicinity of pools (Jones et al., 2018; Sun et al., 2000)—canopy cover may nonetheless provide important benefits to vernal-pool ecosystems and amphibian populations related to wind buffering, leaf-litter inputs, shading effects on water temperature, and dissolved oxygen (Calhoun et al., 2014; Schiesari, 2006; Semlitsch & Skelly, 2008; Shoo et al., 2011).

A primary purpose of our model of vernal-pool inundation patterns was to identify the characteristics of pools that might be most likely to serve as hydrologic refugia under droughts and changing climatic conditions. This process identified the most likely refugia from the set of monitored sites (Table 4). However, the defining features of a refugium may vary depending on location and management focus (e.g., species of interest), so we provide a website for exploring multiple possible definitions of refugia depending on geography, seasonal timing, and management context and objectives (Cartwright, 2020). For example, the greater prevalence of refugia among more northerly pools using predicted wetness probability on July 1 (Table 4) likely reflects climatic influence on timing of snowmelt and pool drying more than any special characteristics of these pools per se. Using the website (Cartwright, 2020), managers may wish to adjust dates of interest depending on pool geography to reflect such climatic gradients in the timing of pool drying.

Ultimately, we view these efforts as only a first step in the larger process of identifying and conserving pools that could function as hydrologic refugia for amphibians of conservation concern. Although many questions remain concerning the potential function of hydrologic refugia in supporting amphibian species persistence under climate change, existing knowledge can help identify hypotheses and research needs. Even without identifying specific refugia from a known set of surveyed sites (as we do here), a landscape with a diversity of pool sizes and hydroperiods is expected to maximize the probability that some pools within a protected area could serve as refugia during droughts or other adverse climatic conditions (Dodd, 1994; Shoo et al., 2011), lending support to calls to conserve diverse types and sizes of wetlands (Babbitt et al., 2003; Calhoun et al., 2017; Snodgrass et al., 2000). Our findings support the notion that larger pools and/or those with generally longer hydroperiods may be more likely to function as hydrologic refugia under droughts or climate change (Baldwin et al., 2006; Brooks, 2009). However, we stress that smaller 'dry-end' wetlands also serve important ecological functions and should not be considered expendable (Calhoun et al., 2003; Snodgrass et al., 2000). Beyond hydrologic suitability, a number of other pool characteristics may be important in determining wetland refugial capacity, including water quality, presence of disease agents, surrounding land use, and legal protections or lack thereof (Babbitt et al., 2009; Calhoun et al., 2003; Daszak et al., 2005; Evans et al., 2017; McLaughlin & Cohen, 2013).

Application of our results to natural-resource management requires a few caveats. Because vernal pools were located using a probabilistic design (Van Meter et al., 2008), our results for the controls on vernal-pool hydrology are robust. However, in evaluating the relative resistance of pools to climate change, only known pool locations can be evaluated as refugia. Each of the protected areas likely has a substantially greater number of vernal pools than were sampled for this study (e.g., 89 pools at the Patuxent Research Refuge, Table 4; whereas Van Meter et al., 2008, estimated that there are around 2200 pools on this Refuge). Decisions to manage or protect only those sites identified here—and in the interactive website (Cartwright, 2020)—would thus be missing many other potential

refugia. Further, careful consideration must be given to protect both climate-buffered habitat patches and connectivity among them to maintain persistent metapopulations (Green & Bailey, 2015), necessitating a landscape focus beyond individual refugial pools. Additionally, models trained on pool observations from protected areas might not adequately represent pools in other contexts, such as on private lands, with differing levels of hydrologic alteration or surrounding land uses.

Our use of three relatively simplistic weather scenarios and climate variables from ensemble averages across 15 climate models implies that pool-wetness predictions do not capture the full range of possible future hydrologic changes. For example, if future climatic drying exceeds that represented by ensemble averages for the region, then our projected changes in pool inundation could be conservative. Furthermore, if both droughts and storms were to intensify, pool hydrology—and thus availability of amphibian breeding habitat—could respond in complex ways not captured by either the ‘dry’ or ‘wet’ weather scenarios (Walls et al., 2013).

A further set of caveats stems from the fact that models of pool hydrology presented here are statistical, ultimately representing correlations in the dataset rather than proof of causation. While other statistical approaches have also produced successful predictive models of depression wetland hydrology (e.g., Barton et al., 2008; Chandler et al., 2016; Greenberg et al., 2015), process-based hydrologic models offer an alternative approach using a water-budget framework and hydrologic accounting on a fixed (e.g., daily) time step (e.g., Garmendia & Pedrola-Monfort, 2010; Qi et al., 2019; Sun et al., 2006). The mechanistic nature of process-based models enables temporal examination of states and fluxes of water throughout the atmosphere-upland-wetland-groundwater system, which could be useful to test hypotheses and scrutinize findings from this and other studies concerning the drivers of vernal pool-hydrology. However, the process of structuring, parameterizing and calibrating process-based hydrologic models for large numbers of vernal pools at a regional scale could be complicated by issues of process complexity and spatial resolution and complexity (Clark et al., 2017), for example, given the small size of vernal pools and the substantial heterogeneity of their hydrologic responses to climate patterns. Perhaps for these reasons, process-based models have typically been applied to only one or a handful of wetlands at a time (Qi et al., 2019; Sun et al., 2006; Wolfe et al., 2004). Further examination of results from this study, then, could be performed using process-based models at a subsample of vernal pools, ideally spanning the gradient from short-to-long hydroperiods.

The utility of refugia to amphibian metapopulations depends strongly on population responses to shifting mosaics of temporally dynamic breeding habitat. Increased pool drying reduces the connectivity of the network of remaining breeding habitats (Fortuna et al., 2006). The extent to which this affects metapopulation persistence depends on species' capacities for local dispersal and migration among increasingly disconnected ‘islands’ of breeding habitat (Compton et al., 2007; Gamble et al., 2007; Werner et al., 2009). For example, Green and Bailey (2015) estimate that at least 50 breeding sites are necessary for metapopulation persistence, but increased isolation will likely increase this minimum number.

As amphibian species respond to climate change through shifts in phenology and geographic ranges (Gibbs & Breisch, 2001; Lawler et al., 2010), research is needed on the relationships between these changes and shifting availability (in both time and space) of breeding habitat. Because amphibians face a variety of threats related to habitat destruction, pathogens and climate change (Rodenhouse et al., 2009; Ryan et al., 2014; Semlitsch & Skelly, 2008; Wake & Vredenburg, 2008), the identification and protection of hydrologic refugia is only one part of a much larger conservation picture.

5 | CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We modelled vernal-pool hydrology across the northeastern United States from a large sample of habitats within Federally protected areas, using thousands of inundation observations collected over more than a decade. Variability in hydroperiod across pools implies potential for some to function as hydrologic refugia from droughts and climate change. Regional-scale models are helpful for identifying pools that could provide refugia but could be strengthened by more detailed data collection at the site scale for hydrologically relevant pool characteristics such as pool substrate and stratigraphy, canopy cover and groundwater fluxes. Better understanding is also needed on how traits of different amphibian species may affect the value of refugia in practice, including dispersal and migration, breeding-site fidelity and phenological shifts.

This and other studies have suggested that earlier pool drying has the potential to affect the availability of breeding habitats across large landscapes, which has important management implications. Conservation strategies that focus on maximizing current-day connectivity among pools may not adequately account for connectivity changes in drying landscapes. In addition to wetland restoration efforts, artificial wetland creation and hydroperiod manipulation may be useful strategies to help support persistence of breeding habitats (Calhoun et al., 2014; Green et al., 2013; Seigel et al., 2006; Shoo et al., 2011). Identifying refugia can be one part of a comprehensive management programme to increase the probability of amphibian persistence.

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DATA AVAILABILITY STATEMENT

Data and R processing scripts used in this study are available from Cartwright, Morelli, and Grant (2020).

ORCID

Jennifer Cartwright  <https://orcid.org/0000-0003-0851-8456>

Toni Lyn Morelli  <https://orcid.org/0000-0001-5865-5294>

Evan H. Campbell Grant  <https://orcid.org/0000-0003-4401-6496>

REFERENCES

- Abatzoglou, J. T., McEvoy, D. J., & Redmond, K. T. (2017). The west wide drought tracker: Drought monitoring at fine spatial scales. *Bulletin of the American Meteorological Society*, 98(9), 1815–1820. <https://doi.org/10.1175/BAMS-D-16-0193.1>
- AdaptWest Project. (2015). Gridded current and future climate data for North America at 1 km resolution. Retrieved October 5, 2018, from <https://adaptwest.databasin.org/pages/adaptwest-climatena>
- Ahmadalipour, A., Moradkhani, H., & Svoboda, M. (2017). Centennial drought outlook over the CONUS using NASA-NEX downscaled climate ensemble. *International Journal of Climatology*, 37(5), 2477–2491. <https://doi.org/10.1002/joc.4859>
- Amburgey, S. M., Murphy, M., & Funk, W. C. (2016). Phenotypic plasticity in developmental rate is insufficient to offset high tadpole mortality in rapidly drying ponds. *Ecosphere*, 7(7), 1–14. <https://doi.org/10.1002/ecs2.1386>
- Babbitt, K. J., Baber, M. J., Childers, D. L., & Hocking, D. (2009). Influence of agricultural upland habitat type on larval anuran assemblages in seasonally inundated wetlands. *Wetlands*, 29(1), 294–301. <https://doi.org/10.1672/07-228.1>
- Babbitt, K. J., Baber, M. J., & Tarr, T. L. (2003). Patterns of larval amphibian distribution along a wetland hydroperiod gradient. *Canadian Journal of Zoology*, 81(9), 1539–1552. <https://doi.org/10.1139/z03-131>
- Baldwin, R. F., Calhoun, A. J. K., & DeMaynadier, P. G. (2006). The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes. *Canadian Journal of Zoology*, 84(11), 1604–1615. <https://doi.org/10.1139/Z06-146>
- Barton, C., Andrews, D., & Kolka, R. (2008). Evaluating hydroperiod response in restored Carolina bay wetlands using soil physicochemical properties. *Restoration Ecology*, 16(4), 668–677. <https://doi.org/10.1111/j.1526-100X.2008.00480.x>
- Boven, L., Stoks, R., Forro, L., & Brendonck, L. (2008). Seasonal dynamics in water quality and vegetation cover in temporary pools with variable hydroperiods in Kiskunsag (Hungary). *Wetlands*, 28(2), 401–410. <https://doi.org/10.1672/06-174.1>
- Brooks, R. T. (2000). Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest (“vernal”) ponds in Central Massachusetts, USA. *Wetlands*, 20(4), 707–715. [https://doi.org/10.1672/0277-5212\(2000\)020\[0707:AASVAT\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2000)020[0707:AASVAT]2.0.CO;2)
- Brooks, R. T. (2004). Weather-related effects on woodland vernal pool hydrology and hydroperiod. *Wetlands*, 24(1), 104–114. [https://doi.org/10.1672/0277-5212\(2004\)024\[0104:WEOWVP\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2004)024[0104:WEOWVP]2.0.CO;2)
- Brooks, R. T. (2005). A review of basin morphology and pool hydrology of isolated ponded wetlands: Implications for seasonal forest pools of the northeastern United States. *Wetlands Ecology and Management*, 13(3), 335–348. <https://doi.org/10.1007/s11273-004-7526-5>
- Brooks, R. T. (2009). Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. *Climatic Change*, 95(3–4), 469–483. <https://doi.org/10.1007/s10584-008-9531-9>
- Brooks, R. T., & Hayashi, M. (2002). Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. *Wetlands*, 22(2), 247–255. [https://doi.org/10.1672/0277-5212\(2004\)024\[0234:E\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2004)024[0234:E]2.0.CO;2)
- Cabrera-Guzmán, E., Crossland, M. R., Brown, G. P., & Shine, R. (2013). Larger body size at metamorphosis enhances survival, growth and performance of young cane toads (*Rhinella marina*). *PLoS ONE*, 8(7), e70121. <https://doi.org/10.1371/journal.pone.0070121>
- Calhoun, A., Arrigoni, J., Brooks, R., Hunter, M., & Richter, S. (2014). Creating successful vernal pools: A literature review and advice for practitioners. *Wetlands*, 34(5), 1027–1038. <https://doi.org/10.1007/s13157-014-0556-8>
- Calhoun, A., Walls, T., Stockwell, S., & McCollough, M. (2003). Evaluating vernal pools as a basis for conservation strategies: A Maine case study. *Wetlands*, 23(1), 70–81. [https://doi.org/10.1672/0277-5212\(2003\)023\[0070:EVPAAB\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2003)023[0070:EVPAAB]2.0.CO;2)
- Calhoun, A. J. K., Mushet, D. M., Bell, K. P., Boix, D., Fitzsimons, J., & Isselin-Nondedeu, F. (2017). Temporary wetlands: Challenges and solutions to conserving a “disappearing” ecosystem. *Biological Conservation*, 211, 3–11. <https://doi.org/10.1016/j.biocon.2016.11.024>
- Cartwright, J., (2020). Vernal pool inundation models. Retrieved September 3, 2020, from <https://www.usgs.gov/centers/lmg-water/science/vernal-pool-inundation-models>
- Cartwright, J., Dwire, K. A., Freed, Z., Hammer, S. J., McLaughlin, B., Misztal, L. W., ... Stevens, L. E. (2020). Oases of the future? Springs as potential hydrologic refugia in drying climates. *Frontiers in Ecology and the Environment*, 18(5), 245–253. <https://doi.org/10.1002/fee.2191>
- Cartwright, J., Morelli, T., & Grant, E. (2020). Inundation observations and inundation model predictions for vernal pools of the northeastern United States: U.S. Geological Survey data release. Retrieved September 4, 2020, from U.S. Geological Survey data release website: <https://doi.org/10.5066/P9CP2NUD>
- Cartwright, J., & Wolfe, W. J. (2016). Insular ecosystems of the southeastern United States: A regional synthesis to support biodiversity conservation in a changing climate. US Geological Survey Professional Paper 1828. Retrieved from <https://doi.org/10.3133/pp1828>
- Chandler, H. C., McLaughlin, D. L., Gorman, T. A., McGuire, K. J., Feaga, J. B., & Haas, C. A. (2017). Drying rates of ephemeral wetlands: Implications for breeding amphibians. *Wetlands*, 37(3), 545–557. <https://doi.org/10.1007/s13157-017-0889-1>
- Chandler, H. C., Rypel, A. L., Jiao, Y., Haas, C. A., & Gorman, T. A. (2016). Hindcasting historical breeding conditions for an endangered salamander in ephemeral wetlands of the southeastern USA: Implications of climate change. *PLoS ONE*, 11(2), 1–17. <https://doi.org/10.1371/journal.pone.0150169>
- Clark, M. P., Bierkens, M. F. P., Samaniego, L., Woods, R. A., Uijlenhoet, R., Bennett, K. E., Pauwels, V. R. N., Cai, X., Wood, A. W., & Peters-Lidard, C. D. (2017). The evolution of process-based hydrologic models: Historical challenges and the collective quest for physical realism. *Hydrology and Earth System Sciences*, 21(7), 3427–3440. <https://doi.org/10.5194/hess-21-3427-2017>
- Compton, B. W., McGarigal, K., Cushman, S., & Gamble, L. R. (2007). A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conservation Biology*, 21(3), 788–799. <https://doi.org/10.1111/j.1523-1739.2007.00674.x>
- Daly, C., Neilson, R., & Phillips, D. (1994). A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology*, 33, 140–158. <https://doi.org/10.1002/asl.228>
- Daszak, P., Scott, D. E., Kilpatrick, A. M., Faggioni, C., Gibbons, J. W., & Porter, D. (2005). Amphibian population declines at Savannah River site are linked to climate, not chytridiomycosis. *Ecology*, 86(12), 3232–3237. <https://doi.org/10.1890/05-0598>
- Davis, C. L., Miller, D. A. W., Grant, E. H., Halstead, B. J., Kleeman, P. M., Walls, S. C., & Barichivich, W. J. (2019). Linking variability in climate to wetland habitat suitability: Is it possible to forecast regional responses from simple climate measures? *Wetlands Ecology and Management*, 27(1), 39–53. <https://doi.org/10.1007/s11273-018-9639-2>
- Davis, J., Pavlova, A., Thompson, R., & Sunnucks, P. (2013). Evolutionary refugia and ecological refuges: Key concepts for conserving Australian

- arid zone freshwater biodiversity under climate change. *Global Change Biology*, 19(7), 1970–1984. <https://doi.org/10.1111/gcb.12203>
- De'ath, G. (2007). Boosted regression trees for ecological modeling and prediction. *Ecology*, 88(1), 243–251. [https://doi.org/10.1890/0012-9658\(2007\)88\[243:BTfEMA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[243:BTfEMA]2.0.CO;2)
- Dodd, K. (1994). The effects of drought on population structure, activity, and orientation of toads (*Bufo quercicus* and *B. terrestris*) at a temporary pond. *Ethology Ecology and Evolution*, 6(3), 331–349. <https://doi.org/10.1080/08927014.1994.9522985>
- Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, 77(4), 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>
- Evans, J. P., Cecala, K. K., Scheffers, B. R., Oldfield, C. A., Hollingshead, N., Haskell, D. G., & McKenzie, B. (2017). Widespread degradation of a vernal pool network in the southeastern United States: Challenges to current and future management. *Wetlands*, 37(1–11), 1093–1103. <https://doi.org/10.1007/s13157-017-0943-z>
- Faccio, S. D., Macfaden, S. W., Lambert, J. D., Neil, J. O., & Mcfarland, K. P. (2016). *The North Atlantic vernal pool data cooperative: Final report submitted to the North Atlantic landscape conservation cooperative*. North Atlantic Landscape Conservation Cooperative.
- Fortuna, M. A., Gomez-Rodríguez, C., & Bascompte, J. (2006). Spatial network structure and amphibian persistence in stochastic environments. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1429–1434. <https://doi.org/10.1098/rspb.2005.3448>
- Gamble, L. R., McGarigal, K., & Compton, B. W. (2007). Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. *Biological Conservation*, 139(3–4), 247–257. <https://doi.org/10.1016/j.biocon.2007.07.001>
- Garmendia, A., & Pedrola-Monfort, J. (2010). Simulation model comparing the hydroperiod of temporary ponds with different shapes. *Limnetica*, 29(1), 145–152.
- Gibbs, J. P., & Breisch, A. R. (2001). Climate warming and calling phenology of frogs near Ithaca, New York, 1900–1999. *Conservation Biology*, 15(4), 1175–1178. <https://doi.org/10.1046/j.1523-1739.2001.0150041175.x>
- Gleeson, T., Moosdorf, N., Hartmann, J., & VanBeek, L. (2014). A glimpse beneath earth's surface: GLObal HYdrogeology MaPS (GLHYMPS) of permeability and porosity. *Geophysical Research Letters*, 41(April), 3891–3898. <https://doi.org/10.1002/2014GL059856>
- Golladay, S. W., Taylor, B. W., & Palik, B. J. (1997). Invertebrate communities of forested limesink wetlands in Southwest Georgia, USA: Habitat use and influence of extended inundation. *Wetlands*, 17(3), 383–393. <https://doi.org/10.1007/BF03161428>
- Grant, E. H. C. (2005). Correlates of vernal pool occurrence in the Massachusetts, USA landscape. *Wetlands*, 25(2), 480–487. <https://doi.org/10.1672/22>
- Green, A. W., & Bailey, L. L. (2015). Using Bayesian population viability analysis to define relevant conservation objectives. *PLoS ONE*, 10(12), e0144786. <https://doi.org/10.1371/journal.pone.0144786>
- Green, A. W., Hooten, M. B., Grant, E. H. C., & Bailey, L. L. (2013). Evaluating breeding and metamorph occupancy and vernal pool management effects for wood frogs using a hierarchical model. *Journal of Applied Ecology*, 50, 1116–1123. <https://doi.org/10.1111/1365-2664.12121>
- Greenberg, C. H., Goodrick, S., Austin, J. D., & Parresol, B. R. (2015). Hydroregime prediction models for ephemeral groundwater-driven sinkhole wetlands: A planning tool for climate change and amphibian conservation. *Wetlands*, 35, 899–911. <https://doi.org/10.1007/s13157-015-0680-0>
- Hargreaves, G., & Allen, R. (2003). History and evaluation of Hargreaves evapotranspiration equation. *Journal of Irrigation and Drainage Engineering*, 129(1), 53–63. [https://doi.org/10.1061/\(ASCE\)0733-9437\(2004\)130:5\(447.2](https://doi.org/10.1061/(ASCE)0733-9437(2004)130:5(447.2)
- Hastie, T., Tibshirani, R., & Friedman, J. (2001). The elements of statistical learning: data mining, inference, and prediction. In *Springer series in statistics*. Springer.
- Hijmans, R., Phillips, S., Leathwick, J., & Elith, J. (2016). *dismo: species distribution modeling*, R package version 1.1–4. Retrieved May 1, 2017, from <https://cran.r-project.org/web/packages/dismo/dismo.pdf>
- Hill, R., Weber, M. H., Leibowitz, S. G., Olsen, A. R., & Thornbrugh, D. J. (2016). The stream-catchment (StreamCat) dataset: A database of watershed metrics for the conterminous United States. *Journal of the American Water Resources Association*, 52(1), 120–128. <https://doi.org/10.1111/1752-1688.12372>
- IPCC. (2013). In T. Stocker, D. Qin, G. Plattner, M. Tignor, S. Allen, J. Boschung, et al. (Eds.), *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge University press. <https://doi.org/10.1017/CBO9781107415324>
- Jones, C. N., McLaughlin, D. L., Henson, K., Haas, C., & Kaplan, D. (2018). From salamanders to greenhouse gases: Does upland management affect wetland functions? *Frontiers in Ecology and the Environment*, 16(1), 14–19. <https://doi.org/10.1002/fee.1744>
- Kinkead, K., & Otis, D. (2007). Estimating superpopulation size and annual probability of breeding for pond-breeding salamanders. *Herpetologica*, 63(2), 151–162. [https://doi.org/10.1655/0018-0831\(2007\)63\[151:essaap\]2.0.co;2](https://doi.org/10.1655/0018-0831(2007)63[151:essaap]2.0.co;2)
- Lawler, J. J., Shafer, S. L., & Blaustein, A. R. (2010). Projected climate impacts for the amphibians of the western hemisphere. *Conservation Biology*, 24(1), 38–50. <https://doi.org/10.1111/j.1523-1739.2009.01403.x>
- Leibowitz, S. G., & Brooks, R. T. (2007). Hydrology and landscape connectivity of vernal pools. In A. Calhoun & P. DeMaynadier (Eds.), *Science and conservation of vernal pools in northeastern North America* (pp. 31–53). CRC Press, LLC. <https://doi.org/10.1201/9781420005394>
- McLaughlin, B., Ackerly, D. D., Klos, P. Z., Natali, J., Dawson, T. E., & Thompson, S. E. (2017). Hydrologic refugia, plants and climate change. *Global Change Biology*, 23, 1–21. <https://doi.org/10.1111/gcb.13629>
- McLaughlin, D. L., & Cohen, M. J. (2013). Realizing ecosystem services: Wetland hydrologic function along a gradient of ecosystem condition. *Ecological Applications*, 23(7), 1619–1631. <https://doi.org/10.1890/12-1489.1>
- Miller, D. A. W., Grant, E. H. C., Muths, E., Amburgey, S. M., Adams, M. J., Joseph, M. B., Waddle, J. H., Johnson, P. T. J., Ryan, M. E., Schmidt, B. R., Calhoun, D. L., Davis, C. L., Fisher, R. N., Green, D. M., Hossack, B. R., Rittenhouse, T. A. G., Walls, S. C., Bailey, L. L., Cruickshank, S. S., ... Sigafus, B. H. (2018). Quantifying climate sensitivity and climate-driven change in north American amphibian communities. *Nature Communications*, 9(1), 1–15. <https://doi.org/10.1038/s41467-018-06157-6>
- Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020). Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, 18(5), 228–234. <https://doi.org/10.1002/fee.2189>
- North Atlantic Landscape Conservation Cooperative. (2014). 2012 Forest above-ground biomass, northeast. Retrieved from 2012 Forest above-ground biomass, northeast website USGS: <https://www.sciencebase.gov/catalog/item/537e207de4b05ed6215c09a9>
- O'Driscoll, M. A., & Parizek, R. R. (2003). The hydrologic catchment area of a chain of karst wetlands in Central Pennsylvania, USA. *Wetlands*, 23(1), 171–179. [https://doi.org/10.1672/0277-5212\(2003\)023\[0171:THCAOA\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2003)023[0171:THCAOA]2.0.CO;2)
- Palis, J. G., Aresco, M. J., & Kilpatrick, S. (2006). Breeding biology of a Florida population of *Ambystoma cingulatum* (Flatwoods salamander)

- during a drought. *Southeastern Naturalist*, 5(1), 1–8. [https://doi.org/10.1656/1528-7092\(2006\)5\[1:bboafp\]2.0.co;2](https://doi.org/10.1656/1528-7092(2006)5[1:bboafp]2.0.co;2)
- Paton, P. W. C., & Crouch, W. B. (2002). Using the phenology of pond-breeding amphibians to develop conservation strategies. *Conservation Biology*, 16(1), 194–204. <https://doi.org/10.1046/j.1523-1739.2002.00260.x>
- Qi, J., Zhang, X., Lee, S., Moglen, G. E., Sadeghi, A. M., & Mccarty, G. W. (2019). A coupled surface water storage and subsurface water dynamics model in SWAT for characterizing hydroperiod of geographically isolated wetlands. *Advances in Water Resources*, 131, 103380. <https://doi.org/10.1016/j.advwatres.2019.103380>
- R Core Team. (2017). R: A language and environment for statistical computing. Retrieved February 1, 2017, from R Foundation for Statistical Computing, Vienna, Austria website: <https://www.r-project.org>
- Ray, A. M., Gould, W. R., Hossack, B. R., Sepulveda, A. J., Thoma, D. P., Patla, D., ... Al-Chokhachy, R. (2016). Influence of climate drivers on colonization and extinction dynamics of wetland-dependent species. *Ecosphere*, 7(7), 1–21. <https://doi.org/10.1002/ecs2.1409>
- Rheinhardt, R., & Hollands, G. G. (2008). Classification of vernal pools: Geomorphic setting and distribution. In A. Calhoun & P. DeMaynadier (Eds.), *Science and conservation of vernal pools in northeastern America* (pp. 12–27). CRC Press, LLC.
- Richter, S. C., Young, J. E., Johnson, G. N., & Seigel, R. A. (2003). Stochastic variation in reproductive success of a rare frog, *Rana sevosia*: Implications for conservation and for monitoring amphibian populations. *Biological Conservation*, 111(2), 171–177. [https://doi.org/10.1016/S0006-3207\(02\)00260-4](https://doi.org/10.1016/S0006-3207(02)00260-4)
- Rodenhouse, N. L., Christenson, L. M., Parry, D., & Green, L. E. (2009). Climate change effects on native fauna of northeastern forests. *Canadian Journal of Forest Research*, 39(2), 249–263. <https://doi.org/10.1139/X08-160>
- Russell, M., Cartwright, J., Collins, G., Long, R., & Eitel, J. (2020). Legacy effects of hydrologic alteration in playa wetland responses to droughts. *Wetlands*. Retrieved from <https://doi.org/10.1007/s13157-020-01334-0>, 40, 2011, 2024
- Ryan, M. E., Palen, W. J., Adams, M. J., & Rochefort, R. M. (2014). Amphibians in the climate vise: Loss and restoration of resilience of montane wetland ecosystems in the western US. *Frontiers in Ecology and the Environment*, 12(4), 232–240. <https://doi.org/10.1890/130145>
- Scheele, B. C., Driscoll, D. A., Fischer, J., & Hunter, D. A. (2012). Decline of an endangered amphibian during an extreme climatic event. *Ecosphere*, 3(11), art101. <https://doi.org/10.1890/es12-00108.1>
- Schiesari, L. (2006). Pond canopy cover: A resource gradient for anuran larvae. *Freshwater Biology*, 51(3), 412–423. <https://doi.org/10.1111/j.1365-2427.2005.01497.x>
- Seigel, R., Dinsmore, A., & Richter, S. (2006). Using well water to increase hydroperiod as a management option for pond-breeding amphibians. *Wildlife Society Bulletin*, 34(4), 1022–1027. [https://doi.org/10.2193/0091-7648\(2006\)34\[1022:uwwtih\]2.0.co;2](https://doi.org/10.2193/0091-7648(2006)34[1022:uwwtih]2.0.co;2)
- Semlitsch, R. (1987). Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. *Copeia*, 1987(1), 61–69. <https://doi.org/10.2307/1446038>
- Semlitsch, R., Scott, D., Pechmann, J., & Gibbons, J. (1996). Structure and dynamics of an amphibian community: Evidence from a 16-year study of a natural pond. In *Long-term studies of vertebrate communities* (pp. 217–248). Academic Press. <https://doi.org/10.1016/b978-012178075-3/50010-6>
- Semlitsch, R., & Skelly, D. (2008). Ecology and conservation of pool-breeding amphibians. In A. Calhoun & P. DeMaynadier (Eds.), *Science and conservation of vernal pools in northeastern America* (Vol. 33) (pp. 127–148). CRC Press, LLC. <https://doi.org/10.2307/2404702>
- Semlitsch, R. D., Scott, D. E., Pechmann, J. H. K., Semlitsch, R. D., Scott, D. E., & Pechmann, J. H. K. (1988). Time and size at metamorphosis related to adult fitness in *Ambystoma Talpoideum*. *Ecology*, 69(1), 184–192. <https://doi.org/10.2307/1943173>
- Shoo, L. P., Olson, D. H., Mccmenamin, S. K., Murray, K. A., Van Sluys, M., Donnelly, M. A., ... Hero, J. M. (2011). Engineering a future for amphibians under climate change. *Journal of Applied Ecology*, 48(2), 487–492. <https://doi.org/10.1111/j.1365-2664.2010.01942.x>
- Snodgrass, J., Komoroski, M., Bryan, A., & Burger, J. (2000). Relationships among isolated wetland size, hydroperiod, and amphibian species richness: Implications for wetland regulations. *Conservation Biology*, 14(2), 414–419. Retrieved from: <http://onlinelibrary.wiley.com/doi/10.1046/j.1523-1739.2000.99161.x/full>
- Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H., & Bradshaw, C. J. A. (2008). Measuring the meltdown: Drivers of global amphibian extinction and decline. *PLoS ONE*, 3(2), 1–8. <https://doi.org/10.1371/journal.pone.0001636>
- Soil Survey Staff. (2016). Gridded Soil Survey Geographic (gSSURGO) Database for the Conterminous United States, version 2.2. Retrieved from Gridded Soil Survey Geographic (gSSURGO) Database for the Conterminous United States, version 2.2 website: <https://gdg.sc.egov.usda.gov/>
- Sun, G., Callahan, T., Pyzoha, J., & Trettin, C. (2006). Modeling the climatic and subsurface stratigraphy controls on the hydrology of a Carolina bay wetland in South Carolina, USA. *Wetlands*, 26(2), 567–580. Retrieved from: [http://link.springer.com/article/10.1672/0277-5212\(2006\)26\[567:MTCASS\]2.0.CO;2](http://link.springer.com/article/10.1672/0277-5212(2006)26[567:MTCASS]2.0.CO;2)
- Sun, G., Riekerk, H., & Kornhak, L. V. (2000). Ground-water-table rise after forest harvesting on cypress-pine Flatwoods in Florida. *Wetlands*, 20(1), 101–112. [https://doi.org/10.1672/0277-5212\(2000\)020\[0101:GWTRAF\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2000)020[0101:GWTRAF]2.0.CO;2)
- Taylor, B. E., Scott, D. E., & Gibbons, J. W. (2006). Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. *Conservation Biology*, 20(3), 792–801. <https://doi.org/10.1111/j.1523-1739.2005.00321.x>
- Theobald, D. M., Harrison-Atlas, D., Monahan, W. B., & Albano, C. M. (2015). Ecologically-relevant maps of landforms and physiographic diversity for climate adaptation planning. *PLoS ONE*, 10(12), e0143619. <https://doi.org/10.1371/journal.pone.0143619>
- Trauth, J., Trauth, S. E., & Johnson, R. L. (2006). Best management practices and drought combine to silence the Illinois chorus frog in Arkansas. *Wildlife Society Bulletin*, 34(2), 514–518. [https://doi.org/10.2193/0091-7648\(2006\)34\[514:bmpadc\]2.0.co;2](https://doi.org/10.2193/0091-7648(2006)34[514:bmpadc]2.0.co;2)
- Trenberth, K. E., Dai, A., van der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2013). Global warming and changes in drought. *Nature Climate Change*, 4(1), 17–22. <https://doi.org/10.1038/nclimate2067>
- US Geological Survey. (2017). 1/3rd arc-second digital elevation models (DEMs)—USGS National map 3DEP downloadable data collection. Retrieved June 29, 2020, from 1/3rd arc-second digital elevation models (DEMs)—USGS National map 3DEP downloadable data collection website: <https://www.sciencebase.gov/catalog/item/4f70aa9fe4b058caae3f8de5>
- USGCRP. (2018). *Impacts, risks, and adaptation in the United States: Fourth national climate assessment, volume II* (D. Reidmiller, C. Avery, D. Easterling, K. Kunkel, K. Lewis, T. Maycock, & C. Stewart, Eds.). Washington DC: U.S. global change research program. USGCRP. <https://doi.org/10.7930/NCA4.2018>
- Van Meter, R., Bailey, L. L., & Campbell Grant, E. H. (2008). Methods for estimating the amount of vernal pool habitat in the northeastern United States. *Wetlands*, 28(3), 585–593. <https://doi.org/10.1672/07-237.1>
- Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*, 23(7), 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *PNAS*, 105, 11466–11473. <https://doi.org/10.17226/12501>

- Walls, S. C., Barichivich, W. J., & Brown, M. E. (2013). Drought, deluge and declines: The impact of precipitation extremes on amphibians in a changing climate. *Biology*, 2(1), 399–418. <https://doi.org/10.3390/biology2010399>
- Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally down-scaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE*, 11(6), 1–17. <https://doi.org/10.1371/journal.pone.0156720>
- Werner, E. E., Relyea, R. A., Yurewicz, K. L., Skelly, D. K., & Davis, C. J. (2009). Comparative landscape dynamics of two anuran species: Climate-driven interaction of local and regional processes. *Ecological Monographs*, 79(3), 503–521. <https://doi.org/10.1890/08-1047.1>
- Wolfe, W., Evans, J., McCarthy, S., Gain, W., & Bryan, B. (2004). *Tree-regeneration and mortality patterns and hydrologic change in a forested karst wetland—Sinking pond, Arnold air Force Base, Tennessee water-resources investigations report 03-4217*. US Geological Survey.
- Yang, L., Jin, S., Danielson, P., Homer, C., Gass, L., Bender, S. M., Case, A., Costello, C., Dewitz, J., Fry, J., Funk, M., Granneman, B., Liknes, G. C., Rigge, M., & Xian, G. (2018). A new generation of the United States National Land Cover Database: Requirements, research priorities, design, and implementation strategies. *ISPRS Journal of Photogrammetry and Remote Sensing*, 146(May), 108–123. <https://doi.org/10.1016/j.isprsjprs.2018.09.006>
- Zedler, P. H. (2003). Vernal pools and the concept of “isolated wetlands”. *Wetlands*, 23(3), 597–607. [https://doi.org/10.1672/0277-5212\(2003\)023\[0597:VPATCO\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2003)023[0597:VPATCO]2.0.CO;2)

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