Wetlands
DOI 10.1007/s13157-015-0680-0

ORIGINAL RESEARCH

Hydroregime Prediction Models for Ephemeral Groundwater-Driven Sinkhole Wetlands: a Planning Tool for Climate Change and Amphibian Conservation

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Received: 11 December 2014 / Accepted: 16 July 2015

Abstract Hydroregimes of ephemeral wetlands affect reproductive success of many amphibian species and are sensitive to altered weather patterns associated with climate change. We used 17 years of weekly temperature, precipitation, and water-depth measurements for eight small, ephemeral, groundwater-driven sinkhole wetlands in Florida sandhills to develop a hydroregime predictive model. To illustrate its utility for climate-change planning, we forecasted weekly wetland water-depths and hydroperiods (2012–2060) using our model and downscaled climate data from the CSIRO Mk3.5 Global Circulation Model under an A1B emissions scenario. We then examined how forecasted water depths and hydroperiods might alter reproductive success, and thereby populations, of five anuran species. Precipitation and water-depth from the prior week were significant predictors of water depth. Our model forecasted shallower depths and shortened hydroperiods for most wetlands when used with the CSIRO Mk3.5 A1B scenario. The forecasted hydroregimes would likely provide adequate reproductive opportunity for only one of the five species we examined. We demonstrate the utility of our model in examining how different climate-change scenarios might affect hydroregimes and, indirectly, biological diversity. Climate change uncertainty highlights the importance of retaining multiple, hydrologically diverse wetlands on landscapes to maximize the potential for successful reproduction by species having differing hydroregime requirements.

Keywords Amphibian reproduction · Climate change · Ephemeral wetlands · Groundwater-driven wetlands · Hydroperiod · Hydroregime · Ocala national forest · Predictive models · Sinkhole wetlands

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Introduction

Wetlands are critical in sustaining biological diversity by supporting amphibians, semi-aquatic reptiles, and aquatic macroinvertebrates that in turn serve as prey for both aquatic and terrestrial wildlife. Many amphibian species inhabit adjacent uplands as adults, but require ephemeral wetlands for breeding. Amphibian eggs and larvae are subject to fewer predators in ephemeral wetlands than in aquatic habitats with permanent water regimes. (Semlitsch and Bodie 1998; Zedler 2003). Small (<1 ha), ephemeral wetlands are especially important for supporting high species richness of amphibians (Snodgrass et al. 2000a; Babbitt 2002) and can produce tens of thousands of juvenile anurans in any given year (Pechmann et al. 1989). Periodic drying makes them unsuitable for fish and can reduce populations of aquatic macroinvertebrates that commonly prey on amphibian larvae (Moler and Franz 1987; Brooks 2009).

Hydroregime characteristics of ephemeral wetlands such as duration of inundation (i.e., hydroperiod), water depth, and

Published online: 31 July 2015

frequency and seasonal timing of filling and drying, are critical factors influencing the reproductive success of amphibians and suitability for supporting amphibian diversity (Brooks 2009). The timing, depth, and duration of water in wetlands can affect amphibian assemblages differently because species differ in their breeding season and larval development rate (Snodgrass et al. 2000b; Babbitt et al. 2003). Thus, wetlands that dry during a species' breeding season are unavailable to that species for reproduction. Likewise, wetlands that dry before larval development is complete will result in tadpole deaths and reproductive failure (Pechmann et al. 1989; Brooks 2009; Walls et al. 2013a).

The hydrology of ephemeral wetlands is strongly affected by the amount and timing of precipitation, making them especially sensitive to altered weather patterns resulting from climate change (Brooks 2005, 2009). Despite the great potential for climate change to influence amphibians, global, national, and regional assessments often do not address how small, ephemeral wetlands and the biological diversity they support may be affected by a changing climate.

In the southeastern United States, climate models project a 2–10 °C increase in temperature by 2100 (IPCC 2007), and climate change is already evident. Since the 1970s, mean average temperature in the region has risen by approximately 1 °C, with the greatest seasonal temperature increase during winter (Karl et al. 2009). Drought has also affected much of Southeast over the past three decades, and temporal patterns of precipitation have changed. For example, mean summer precipitation has decreased, whereas mean fall precipitation has increased by 30 % since 1901. Severity and patterns of storms are changing, with more heavy downpours in many parts of the southeast and more powerful Atlantic hurricanes (Karl et al. 2009).

Observed and predicted climate change is not uniform across the southeastern region, suggesting the importance of developing climate change forecasts specific, or downscaled, to physiographic regions or landscapes. Further, climate change forecasts differ considerably depending on the Global Circulation Model (GCM) used and are additionally confounded by future scenarios based on different assumptions about greenhouse gas emissions and population growth. Changes in weather patterns including precipitation amount, frequency, timing, and severity, as well as temperature and atmospheric circulation will almost certainly change hydroperiod characteristics in wetlands, with critical implications for amphibian reproduction. These likely hydroperiod changes highlight the need for models to predict wetland hydrology that can be used with alternative or evolving climate change scenarios for effective amphibian conservation planning at landscape and regional levels.

We used 17 years of weekly (March 1994-August 2011) temperature, precipitation, and water depth measurements to develop predictive models of water depth and hydroperiod for each of eight small (0.1–0.4 ha), ephemeral, groundwater-driven sinkhole wetlands. We also developed a general model using data from all eight wetlands combined. We then applied our models to downscaled climate data for our study area using the CSIRO Mk3.5 Global Circulation Model (GCM) forced by the A1B emissions scenario (IPCC 2007). Lastly, we used hydroregimes for our study wetlands as forecast by our model, and respective breeding seasons and rates of larval development of five common anuran species, to illustrate how climate-change altered hydroregimes could affect local amphibian populations by changing the frequency, season, duration, and depth of water in ephemeral, groundwater-driven sinkhole wetlands.

Methods

Study Area

Our study wetlands were eight small (0.1–0.37 ha), ephemeral, groundwater-driven sinkhole wetlands in longleaf pine-wiregrass sandhills located in the Ocala National Forest, Marion and Putnam Counties, Florida (Fig. 1). Wetland elevations at their approximate lowest point ranged from 4.0 to 26.2 m above mean sea level (AMSL). Average weekly precipitation and depths of study wetlands (March 1994-August 2011) are shown in Fig. 2. Average (1981–2010) annual precipitation at Ocala, Florida was 129 cm, with more than half occurring during late spring and summer (NOAA 2013). Average daily maximum and minimum temperatures were 32.1 and 19 °C during April to October, and 24 °C and 9.4 °C for November to March (NOAA 2013). Heavy precipitation providing groundwater recharge was associated with thunderstorms in late May through early October, tropical systems in summer and fall, and wet autumn, winter, or spring frontal systems (Winsberg 1990). Groundwater recharge can be substantial in winter, when evapotranspiration is low (Knowles et al. 2002).

The topography included dune-like undulations and abundant closed depression sinkholes with limited surface drainage networks (Kalisz and Stone 1984). Here, stratified gravel, sand, and kaolinitic clays of the Citronelle Formation and locally discontinuous or irregular clay layers are overlain by sands of varying thickness (Kalisz and Stone 1984). Ocala Limestone underlies the entire study area. Common soils are well to excessively drained Entisols with <5 % silt plus clay in the upper profile, and are classified in the hyperthermic, uncoated families of Spodic (Paola series) and Typic (Astatula series) Quartzipsamments (Aydelott et al. 1975). Elevations within the study area range from 49 m AMSL in the northern part of the forest to 2 m AMSL near the St. Johns River (Kalisz and Stone 1984).

The Surficial Aquifer System and Floridan Aquifer System are the primary water-bearing sources within the Ocala

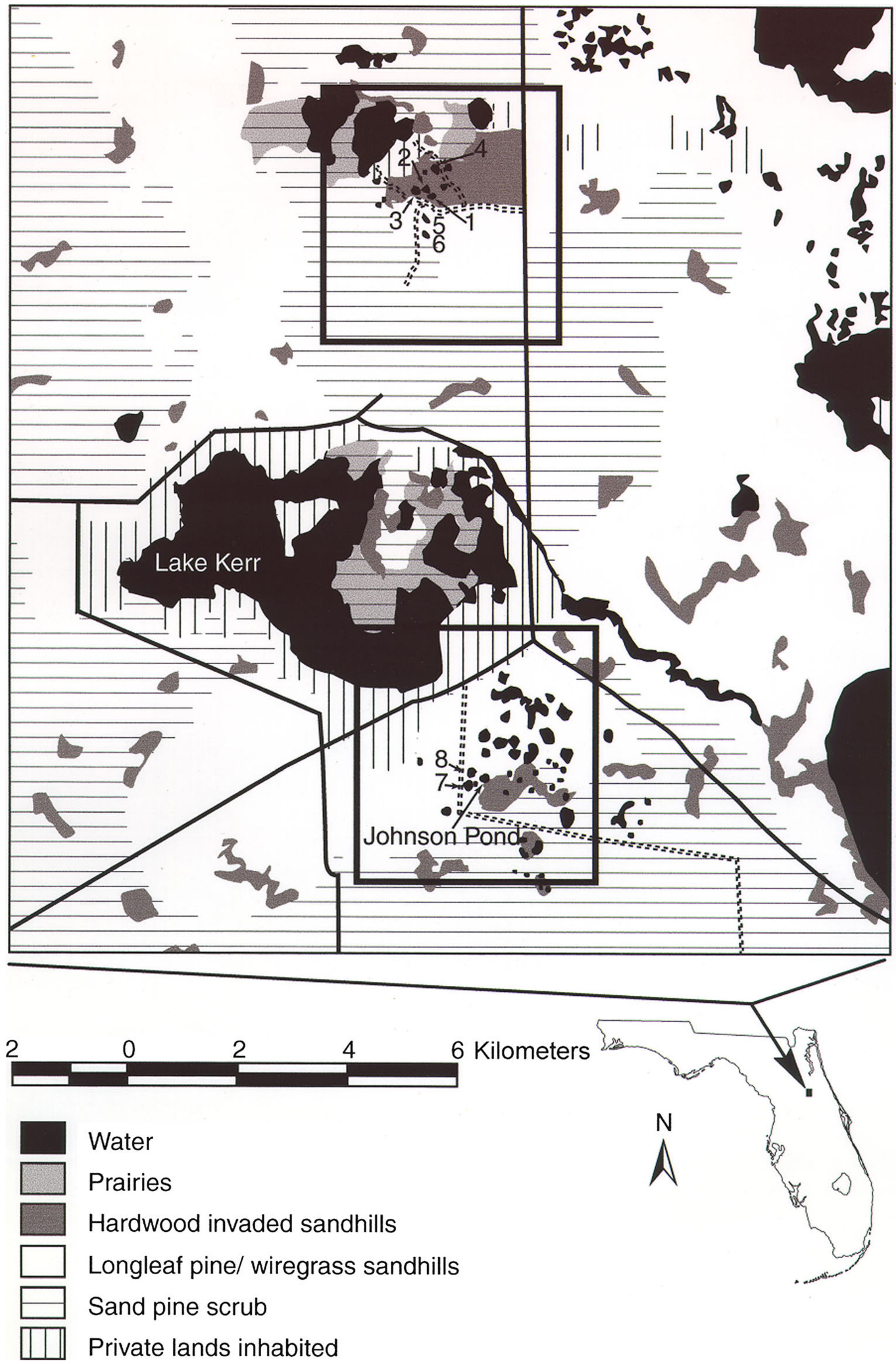

Fig. 1 Locations of study wetlands in the Ocala National Forest, Putnam and Marion Counties, Florida (courtesy of Dale Johnson)

National Forest (Knowles et al. 2002). An intermediate confining unit composed of the Hawthorne Group geologic formations, including phosphatic sand, clay, and limestone with younger low permeable silt and clay beds (Knowles et al. 2002), separates the Surficial and Floridan Aquifer Systems. The confining unit restricts vertical groundwater movement between the two aquifer systems except where breached by sinkholes. Thickness of the intermediate confining unit varies between 0 and 46 m due to past erosion and sinkhole formation. Water levels within the Surficial Floridan Aquifer are driven primarily by precipitation, with the largest increases following consecutive years with above-average precipitation and greatest decreases following consecutive years with below-average precipitation (Knowles et al. 2002).

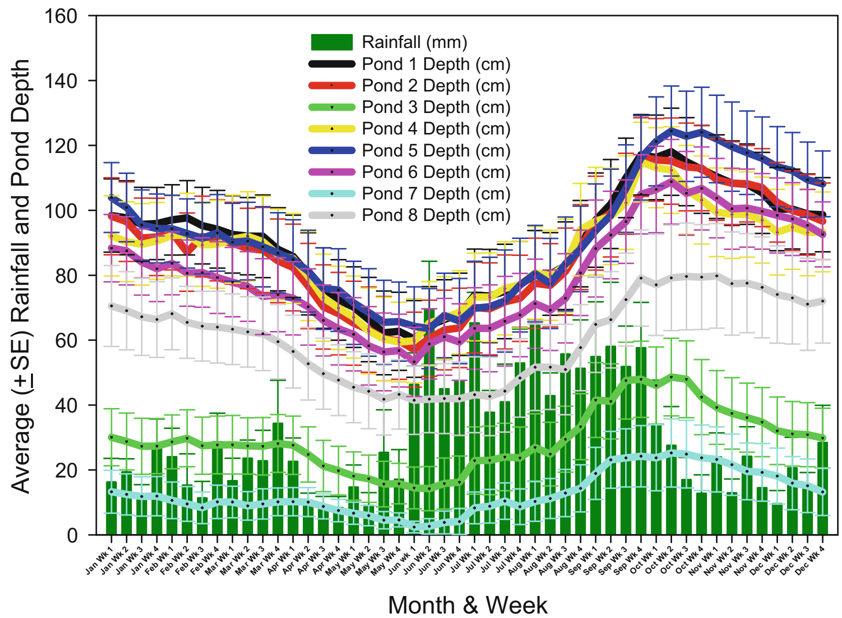

Fig. 2 Mean (±SE) weekly rainfall and water-surface elevations for eight ephemeral, groundwater-driven sinkhole wetlands in the Ocala National Forest, Marion and Putnam Counties, Florida (1994-August, 2011)

Weather and Water Depth Measurements

We measured precipitation and maximum and minimum air temperature within our study area from 28 March 1994 to 27 August 2011. Weather data were recorded daily from late March 1994 – mid-2006 (and summed to weekly totals), and at approximately weekly intervals thereafter except during mid-April through late May (6 weeks) and late December through early January (3 weeks) in 2006. We also measured water depth at depth poles (marked pvc pipes) permanently established at the approximate lowest point within each of the eight wetland basins. Water depths were measured at approximately weekly intervals, except for brief periods during 2008 (14 weeks missing for all wetlands) and 2009 (9 weeks missing for all wetlands and 29 weeks missing for wetland 4).

Hydrology Model Development

Data Structure, Function Selection and Autocorrelation

Our panel dataset (see Greene 2000) consisted of 837 time series observations (weeks; minus some missing values) on each of eight wetlands. The study wetlands can be considered a representative selection of small, ephemeral, groundwater-driven sinkhole wetlands within xeric uplands of the Floridan Aquifer System region. A time series model describes the path of a variable y_t in terms of contemporaneous factors $\mathbf{x}_t$, its own past (lagged dependent variables, i.e. $y_{t-1}, y_{t-2}, \ldots$) and disturbances ε_t, which may exhibit autocorrelation. In the usual time-series setting, the disturbances are assumed to be homoscedastic but follow a first-order autoregression or AR(1) process, $\varepsilon_t = \rho\varepsilon_{t-1} + \nu_t$ where $\nu_t \sim \text{iid}(0, \sigma_\nu^2)$ (Greene 2000).

We explored linear models using stepwise regression procedures to determine a parsimonious and consistent model form to forecast water depth for each of the eight wetlands. With water depth as our dependent variable, we included total precipitation for the current week, total precipitation for current and prior week, date (week/year), minimum weekly temperature, maximum weekly temperature, midrange weekly temperature, and the previous number of weeks when wetland was dry. We did not include calculated evapotranspiration, but instead assumed that the high correlation between temperature and evapotranspiration rendered adequate our temperature measures as a surrogate (Kosa 2011). We also included a first-order lag of water depth (water depth 1 week prior) as a regression variable. To test for serial correlation, we computed values of generalized Durbin-Watson statistics for p=1, 2, 3, and 4.

Linear Mixed Modeling

Our data were based on a sample of multiple measurements taken from different wetlands. This type of nested structure, where each wetland is considered to be a random deviation from some population regression model, is typically modeled as a random coefficients model (Jiang 2010) with the general expression of

$$\mathbf{y} = \mathbf{X} + \mathbf{Z}\gamma + \varepsilon, \tag{1}$$

where $\mathbf{y}$ represents a vector of observed data, $\boldsymbol{\beta}$ is an unknown vector of fixed-effects parameters with known design matrix $\mathbf{X}$, $\boldsymbol{\gamma}$ is an unknown vector of random-effects parameters with known design matrix $\mathbf{Z}$, and ε is an unknown random error vector.

Model Construction and Parameter Effects

During the construction of our mixed model, we estimated: (1) the form of **Z**, that is, which of the parameters in the model will be considered as parameters of a mixed effect, composed of a fixed part (common to all wetlands) and a random part (specific for each wetland), or as parameters of a purely fixed effect; (2) the structure of the among-wetland variance-covariance matrix (**G**); and (3) the within-wetland variance-covariance structure (**R**) for explaining variability of depth through time in the same wetland.

We tested the null hypothesis that the residual variance and autocorrelation do not vary among wetlands (H_0: $\mathbf{R}_1=\mathbf{R}_2=\cdots=\mathbf{R}_8$), versus the alternate hypothesis (H_1) that they do vary among wetlands, or not all $\mathbf{R}_i$ are equal. The null hypothesis implies a reduced model form meaning $\sigma_1^2=\cdots=\sigma_8^2$ and $\rho_1=\cdots=\rho_8$ (or ${}_1 = \cdots = {}_8$, if we determine an AR(p) process is appropriate). The alternate hypothesis implies a full model form meaning the residual variance and autocorrelation vary across wetlands. We used the LRT statistic to test the hypotheses and AIC values were compared.

We first tried fitting the linear mixed model, with intercept, precipitation, and lagged water depth as mixed effects, using PROC MIXED (SAS Institute Inc. 2009) (Jiang 2010) but were unable to achieve model convergence. As the coefficients on lagged water depth had little variability (see Table 2), we entered it into the model as a purely fixed effect. With intercept and precipitation slope as mixed effects, the **G** matrix became a 2× 2 matrix with variance parameters σ_a^2,σ_b^2, and σ_{ab}. We then fit the linear mixed model under two scenarios: (1) a full model, where variance and serial correlation parameters varied across wetlands (each $\mathbf{R}_i$ was different); and (2) a reduced model, where $\mathbf{R}_1=\cdots=\mathbf{R}_8$. The likelihood ratio test (LRT=42699.9–42396.3=303.6 with 14 degrees-of-freedom, $P<0.001$) rejected the null hypothesis that all $\mathbf{R}_i$ were equal. The AIC for the reduced model was 42709.9 whereas the AIC for the full model was smaller at 42434.3 indicating the full model was a better fit to our data.

Model Validation

We validated the general form of the model (Eq. 3) by estimating water depths for wetlands 1 through 6 for the year 2014. Wetlands 7 and 8 were omitted from validation as they were dry for all 2014 measurements. We used a scatterplot to compare observed and predicted water depths.

Climate Change Scenario and GCM Selection

Several alternative emissions scenarios were developed by the Intergovernmental Panel on Climate Change (IPCC 2007) based on broad storylines about future economic, demographic, political, environmental, and technological change (Nakicenovic et al. 2000) and are used to drive GCMs to produce projections of future climatic conditions. We used one potential emissions scenario (A1B) and GCM (CSIRO Mk3.5) with weekly, downscaled climate data for Putnam County, Florida to illustrate how our models could be used to examine potential changes in hydroperiod under alternative climate change scenarios. The A1 scenario family describes a future of very rapid economic growth, a global population that peaks in mid-century and declines thereafter, and rapid introduction of new and more efficient technologies; A1B (within the A1 family) represents a balance between fossil fuels and alternative energy sources (Nakicenovic et al. 2000; Wear et al. 2013). The CSIRO Mk3.5 GCM was developed by the Commonwealth Scientific and Industrial Research Organization of Australia (Gordon et al. 2010).

Developing Weekly Downscaled Climate Data for Putnam County Florida

Output from the CSIRO Mk3.5 GCM was downscaled to our region of interest using an interpolation model (ANUSPLIN) that incorporates four dimensions (climatic variable, latitude, longitude, and elevation) to produce gridded surfaces for both monthly precipitation and surface air temperature with a grid spacing of 1/12° (Hutchinson 2007). To arrive at a climate projection for Putnam County, Florida, we used the grid point in the downscaled gridded data closest to the center of the county.

We transformed monthly climate scenarios into the weekly time series required for the water depth models using information from the weather observations used in developing the statistical water depth model. We calculated average maximum temperature and total precipitation for each month in the observed data. For each week, the mean maximum temperature for the month was subtracted from the week's temperature to create anomaly values, and precipitation values were divided by the total monthly precipitation for the month to provide fractions of total monthly precipitation for each week. Once the observed values were scaled in this manner, an artificial time-series of scaled values was generated by randomly selecting with replacement from a pool of candidate months. The observed data covered the period of late March 1994 through late August 2011, providing 17 potential weekly patterns for each month. This pool was further expanded by randomly shuffling the weeks when a month was selected. This random selection process was repeated to produce a time series of scaled values covering the period 2000 through 2060. The same, scaled time-series was then combined with the monthly temperature and precipitation data for the selected scenarios to produce a weekly time series for each. As each climate scenario shares similar structure on a weekly level, changes in wetland water levels will reflect changes in the mean climate rather than changes in periodicity of weather events.

Determining Hydroperiod Characteristics Required by Five Anuran Species

We used published literature (Ashton and Ashton 1988; Greenberg 2001; Greenberg and Tanner 2004, 2005a, b) and capture data from our study wetlands to define both minimum and optimum timing and duration of hydroperiod required to breed and successfully recruit juveniles for five anuran species (*Anaxyrus quercicus*, *A. terrestris*, *Gastrophryne carolinensis, Lithobates capito*, and *Scaphiopus holbrookii*). These reproductive requirements were based on breeding season and rate of larval development to metamorphosis for each of the five species (Table 1). We then compared the number of years (2012–2060) forecasted with our wetland hydrology models using the CSIRO Mk3.5 GCM forced by the A1B climate change scenario, when minimum and optimum hydroperiod requirements were met for each anuran species by wetland. We were unable to find information on minimum water depths required for tadpole development except in relation to increased inter- and intraspecific competition and predation rates as wetlands dry, reducing reproductive success (e.g., Brendonck et al. 2002). Therefore, our "minimum" cutoff is conservative (e.g. our defined minimum 1 cm depth may be inadequate, thus estimates of "suitable" hydroperiods overestimated).

Results

Wetland Hydrology Model Results

Function Selection

The stepwise procedures and additional analyses (e.g., correlation analyses and plots of water depth against potential independent variables) pointed to the same linear model form for each wetland:

$$d_{it} = \beta_{i0} + \beta_{i1} r_{it} + \beta_{i2} d_{i,t-1} + \varepsilon_{it}, \qquad (2)$$

where d_{it} is the water depth (cm) of the *i*th wetland at the *t*th time period, r_{it} is measured precipitation (cm) for the *i*th wetland at the *t*th time period, $d_{i,t-1}$ is water depth lagged one time period (first-order lagged dependent variable), the β's are regression parameters and $_i$ represents an AR(1) disturbance vector for the *i*th wetland. Residual plots showed errors are homoscedastic. Statistics and parameter estimates for each wetland model are given in Table 2.

There was close agreement between observed and predicted values (Table 2) as evidenced by the high coefficients of determination (0.967 to 0.988). There was high variability in intercepts (−1.006 to −3.922) and slope values (0.399 to 1.642) for precipitation. This gives strong evidence for random effects influencing intercepts and precipitation slope. By contrast, the slope values on the lagged water depth were very similar (0.9836 to 0.9972). The regression mean square error values had almost a 3-fold spread ranging from 23.99 to 65.94 cm^2. The generalized Durbin-Watson tests showed that the majority of the wetland regressions exhibited a first-order autoregression, or AR(1), disturbance process. Therefore, for the linear mixed model we used an AR(1) process in the specification for the **R** matrix.

Linear Mixed Model

The general equation for the linear mixed model is

$$\hat{d}_{it} = \hat{\beta}_0 + \hat{\gamma}_{i0} + \left(\hat{\beta}_1 + \hat{\gamma}_{i1}\right) r_{it} + \hat{\beta}_2 d_{i,t-1}. \qquad (3)$$

This equation, using the appropriate parameter estimates as given in Table 3, was used to forecast water depth for each wetland under the different climate scenarios and GCMs. Note that there are a few random-effects parameters that are not significant using α=0.05, and theoretically they could be dropped from the model [i.e., the values would be set to 0 in Eq. (3)]. However, we chose to retain them (this provides protection against Type II errors) for our forecasts under the

Table 1 Minimum and optimum hydroregime (duration and season of hydroperiod ≥1 cm depth) required by five anuran species for successful juvenile recruitment

Species	Minimum hydroperiod and timing	Optimum hydroperiod and timing
Anaxyrus quercicus	Any 4 weeks continuous	Continuous
	May week 4–Sept week 2	May week 3–Sept week 2
A. terrestris	Any 6 weeks continuous	Continuous
	March week 1–Aug week 2	Feb week 2–Aug week 2
Gastrophryne carolinensis	Continuous	Continuous
	Jun week 4–Aug week 2	May week 3–Oct week 4
Lithobates capito	Any 14 weeks continuous Jan week 2–Sept week 3	Year-around
Scaphiopus holbrookii	Any 3 weeks continuous IF	Any 3 weeks continuous IF
	Heavy rain (≥8.6 cm within a single week)	Heavy rain (≥8.6 cm within a single week)
	+ Dry within 8 weeks prior to heavy rains	+ Dry within 8 weeks prior to heavy rains

Table 2 Results for exploratory regressions of water depths for eight ephemeral wetlands in the Ocala National Forest, Florida: parameter estimates (SE), mean square error ($\hat{\sigma}^2$), coefficient of determination (R^2), generalized Durbin-Watson (DW) statistic (AR order in parenthesis), and probability (P) value associated with the DW test

Wetland	$\hat{\beta}_0$	$\hat{\beta}_1$	$\hat{\beta}_2$	$\hat{\sigma}^2$	R^2	DW	P
1	3.689 (0.469)	1.351 (0.052)	0.9944 (0.0042)	39.42	0.986	2.13 (1)	0.038
2	−3.922 (0.572)	1.538 (0.066)	0.9899 (0.0052)	62.30	0.979	2.43 (1)	<0.001
3	−2.608 (0.324)	0.997 (0.053)	0.9836 (0.0058)	40.75	0.974	1.85 (2)	0.015
4	−3.957 (0.553)	1.642 (0.065)	0.9891 (0.0051)	58.77	0.980	2.24 (1)	<0.001
5	−2.986 (0.6060)	1.137 (0.068)	0.9934 (0.0052)	65.94	0.978	1.81 (1)	0.003
6	−3.154 (0.546)	1.261 (0.063)	0.9911 (0.0053)	57.24	0.978	2.18 (1)	0.006
7	−1.006 (0.229)	0.399 (0.041)	0.9844 (0.0064)	23.99	0.967	1.78 (3)	0.001
8	−2.283 (0.356)	0.766 (0.049)	0.9972 (0.0040)	34.73	0.988	1.79 (2)	0.002

climate scenarios. The linear mixed model can be used without the random-effects parameter estimates (e.g., the general form of the model) to generate water depth predictions for any small, ephemeral, groundwater-driven sinkhole wetland within xeric uplands of the Floridan Aquifer System region because the fixed-effects parameter estimates $\left(\hat{\beta}\right)$ in Eq. (3) represent a population level mean-response equation (Table 3).

Model Validation

We validated the general form of the model (Eq. 3) by estimating water depths for wetlands 1 through 6 for the year 2014. Wetlands 7 and 8 were omitted from validation as they were dry for all 2014 measurements. We used a scatterplot to compare observed to predicted water depths (Fig. 3). The model accounted for approximately 76 % of the variance present in 2014 water depths. The observed mean water depth across all wetlands in 2014 was 50.6 cm while the predicted mean was 39.3 cm. Root mean squared error between predictions and observations was 17.0 cm. Comparison of the distributions of predicted and observed water depths reveals that the simulated water depths are not as high and have more occurrences of water depth in the 10 to 30 cm range than observed (Fig. 4).

Future Precipitation and Temperature Projections for Putnam County Florida

Quartiles of observed maximum temperature by month and annual cumulative precipitation by month for Putnam County provide context for our projections of future climatic conditions (Fig. 5). Temperatures tend to show greater variability during the winter as the lowest quartile expands in range. While Putnam County gets precipitation throughout the year, the late spring and summer months are when the area receives the majority of its precipitation

Table 3 Fixed-effects (used in the general model) and random-effects (used with fixed-effects for individual study wetlands) parameter estimates, standard errors (SE), and significance tests for the linear mixed model (Eq. 3) of ephemeral, groundwater-driven sinkhole wetland depth, Ocala National Forest, Florida

Specification	Parameter	Estimate	SE	t value	P
Fixed-effects parameters	β_0	−3.141	0.405	−7.76	<0.001
	β_1	1.150	0.149	7.74	<0.001
	β_2	0.994	0.0008	1322	<0.001
Random-effects parameters	γ_{10}	−0.738	0.350	−2.11	0.035
	γ_{11}	0.260	0.154	1.68	0.092
	γ_{20}	−1.065	0.366	−2.91	0.004
	γ_{21}	0.418	0.156	2.68	0.008
	γ_{30}	0.558	0.350	1.59	0.111
	γ_{31}	−0.137	0.155	−0.88	0.377
	γ_{40}	−1.425	0.375	−3.80	<0.001
	γ_{41}	0.497	0.157	3.17	0.002
	γ_{50}	0.178	0.398	0.45	0.654
	γ_{51}	−0.0779	0.159	−0.49	0.624
	γ_{60}	−0.401	0.374	−1.07	0.284
	γ_{61}	0.127	0.157	0.81	0.419
	γ_{70}	1.894	0.292	6.49	<0.001
	γ_{71}	−0.722	0.152	−4.75	<0.001
	γ_{80}	0.999	0.337	2.97	0.003
	γ_{81}	−0.366	0.154	−2.38	0.017

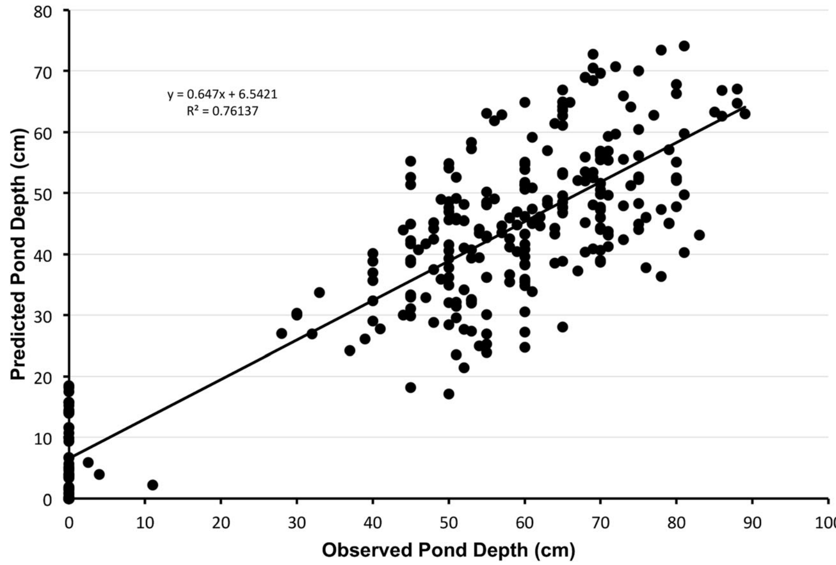

Fig. 3 Scatterplot of observed water depths (2014) and predicted water depths of eight ephemeral, groundwater-driven depression wetlands in the Ocala National Forest, Marion and Putnam Counties, Florida

each year. In contrast to the fairly symmetric distribution for maximum temperatures, the distribution of cumulative precipitation is negatively skewed.

The future distribution of temperatures for Putnam County from the CSIRO Mk3.5 projection for the A1B emissions scenario reveals cooler winter temperatures (Fig. 5). The 50th percentile line for cumulative precipitation is very close to the observed 50th percentile, but the model accumulates precipitation in a linear fashion compared to the observed precipitation pattern. The CSIRO Mk3.5 projections suggest that the wettest years in the future could be much wetter than current conditions.

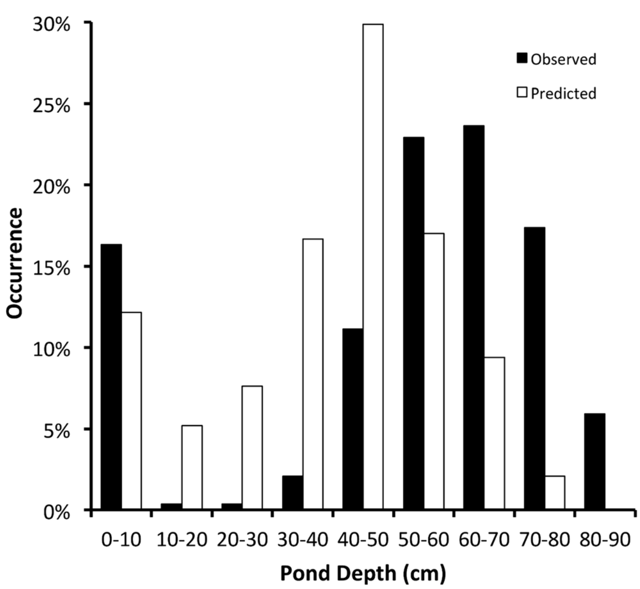

Fig. 4 Comparison of observed and predicted water depths for 2014 for eight ephemeral, groundwater-driven sinkhole wetlands in the Ocala National Forest, Marion and Putnam Counties, Florida

Forecasted Hydroperiods: Implications for Amphibian Reproductive Success

Figure 6 illustrates the application of our hydrology models to forecast (2012–2060) hydroperiod characteristics at study wetlands based on downscaled climate data. Under the CSIRO Mk3.5-A1B climate change scenario, sufficiently frequent (one to several within the lifespan of the species) hydroperiods meeting reproductive requirements for *S. holbrookii* were forecast for most wetlands (Fig. 7). In contrast, forecasted minimum and optimum hydroperiods were insufficiently frequent for *A. quercicus*, *A. terrestris*, *L. capito*, and *G. carolinensis* reproduction (Fig. 7), with multiple continuous years of no or few even minimally suitable hydroperiods at most study wetlands (e.g. 2026–2042).

Discussion

Our general linear mixed model (Eq. 3 without the random-effects parameters specific to each study wetland) can be used with different climate change scenarios and GCMs to generate weekly water depth predictions for any small, ephemeral, groundwater-driven sinkhole wetland within xeric uplands of the Floridan Aquifer System region because the fixed-effects parameter estimates (̂) represent a population level mean-response equation. The model also calculated below-ground pond depths; although we did not measure below-ground water levels in the field (dry ponds were recorded as 0 cm depth), we assumed that negative pond depths calculated in our model were acceptable, since the linear model was reasonably good. The simplicity of our model makes it a valuable tool for land managers, planners, and scientists interested in examining how changes in weather patterns associated with

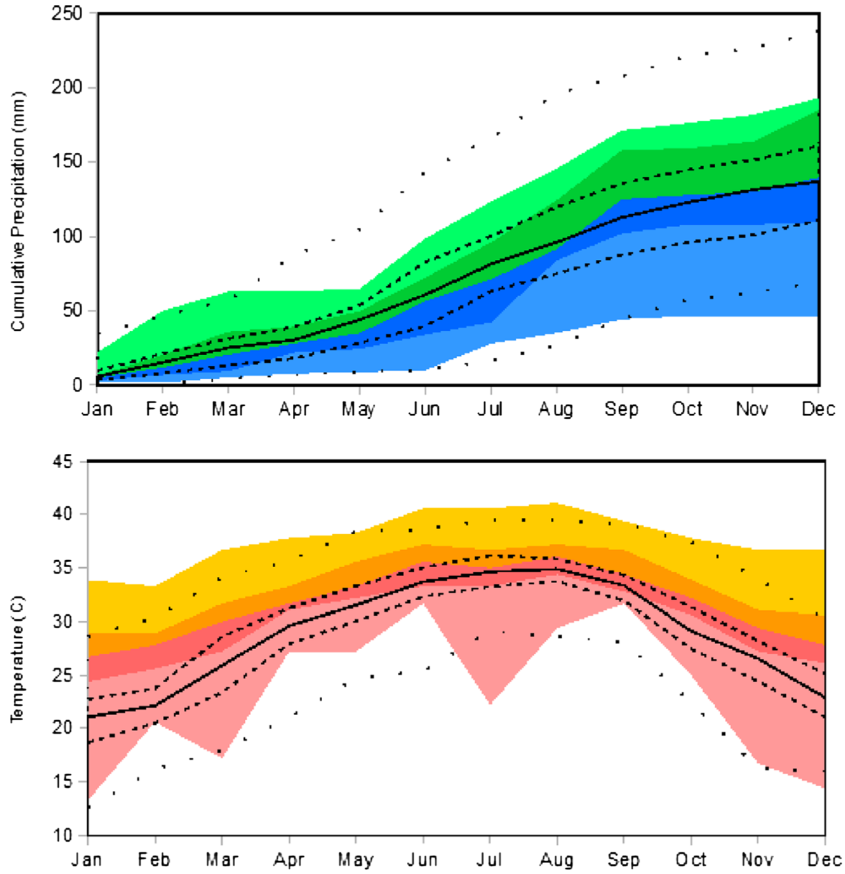

Fig. 5 Quartiles of maximum monthly temperature (*top*) and cumulative precipitation (*bottom*) using the CSIRO Mk3.5-A1B climate change scenario. *Dotted lines* for 0 and 100th percentile; *dashed* for 25th and 75th; *solid* for 50th overlaid on historical quartiles (colored bands, each representing 25 %) of observed maximum temperature and annual cumulative precipitation for Putnam County, Florida, 1994–2011

climate change will potentially affect hydroperiods of groundwater-driven sinkhole wetlands such as the ones we studied, and populations, communities, and sustainability of amphibians or other species dependent on these ephemeral wetlands.

Our models indicated that only precipitation and water depth the prior week (lag) were significant predictors of current water depth. Elevation was not a significant predictor, indicating that on this landscape groundwater flow was not level. Knowles et al. (2002) reported that surface topography influences water flow of the Surficial Aquifer System in a "subdued manner," but subsurface drainage influenced by karst features and vertical leakage of water to or from the Upper Floridan Aquifer also affect groundwater flow in the Ocala National Forest. Sun et al. (2006) also reported that groundwater flow in a Carolina bay was not governed solely by land surface topography but was influenced by the underlying hydrologic restricting layer beneath the wetland-upland continuum. Differences between observed and predicted water depths seen in our model validation are likely due to the simplicity of the model and its incomplete description of hydrology of the Floridan Aquifer System.

Surprisingly, temperature (weekly minimum, maximum, or midrange), which we assumed to be a surrogate metric for evapotranspiration, also was not an important predictor of water depth in our study. Other studies in the eastern US have found that evapotranspiration plays an important role in some types of ephemeral wetlands (e.g. vernal pools in New England (Brooks 2009); Carolina bays in the Middle Coastal Plain of South Carolina (Sun et al. 2006); depression wetlands, or karst pans on the Tennessee Highland Rim (Hill et al. 2006); and cypress ponds within a Florida pine flatwoods forest (Mansell et al. 2000)). Our result may be due to factors other than precipitation (source) and evaporation (loss) adding complexity to simple hydrology models assuming an impervious basin. Precipitation over a larger area must be considered, as runoff and groundwater flow also contribute to water depth. Additionally, while temperature is still a reasonable surrogate for evapotranspiration, the relationship is not simple; at high temperatures plants can alter their rate of water loss. The complexity of factors affecting groundwater movement into or from wetlands, and water use by plants apparently minimized the relative importance of temperature in our models.

We used one of many available climate projections to illustrate how our wetland hydrology models can be used to test alternative and constantly evolving climate scenarios; we do not suggest that this scenario will actually occur. In fact, different emissions scenarios, GCMs, and climate data downscaling methods can produce markedly different climate

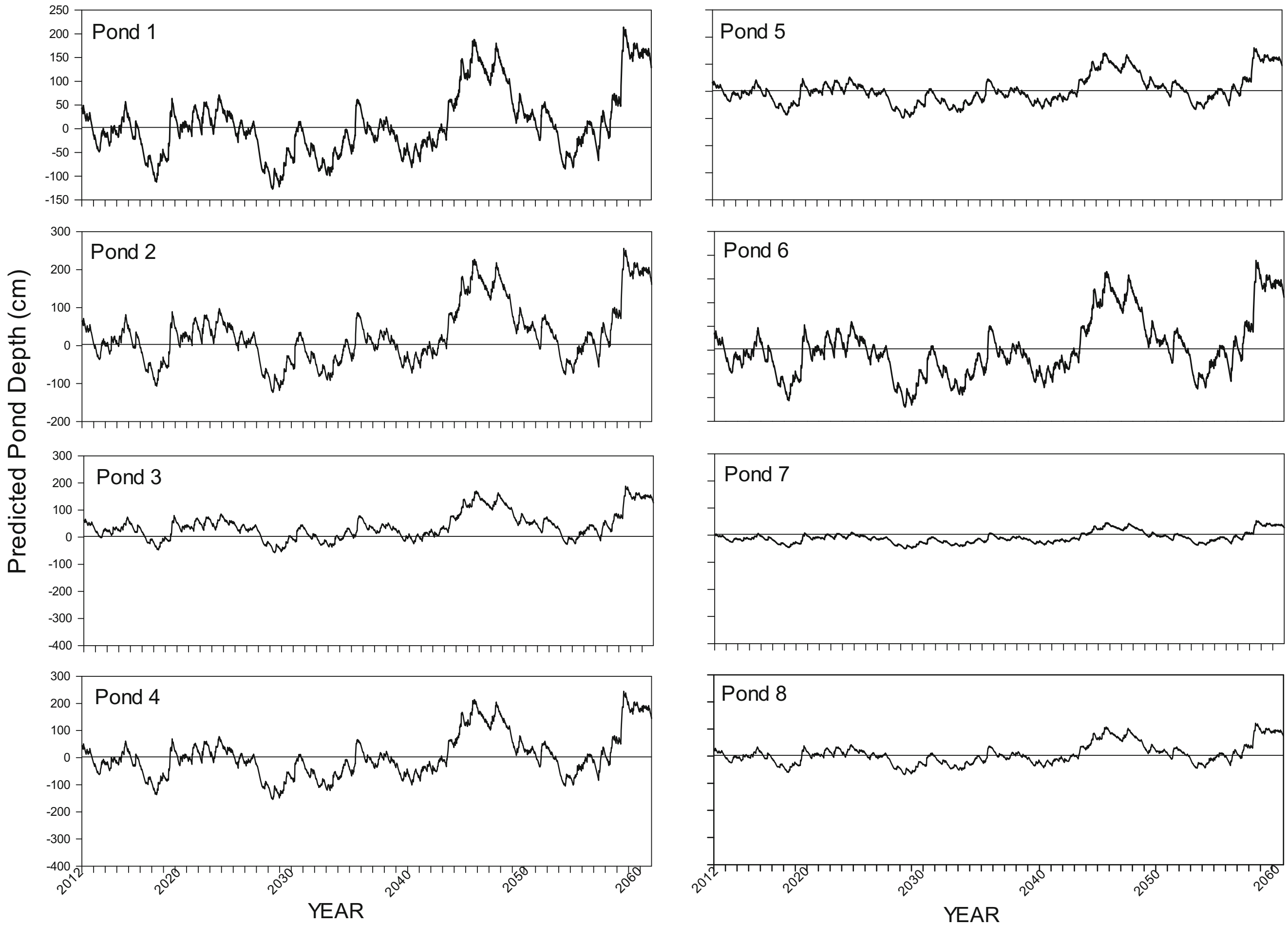

Fig. 6 Forecasted (2011–2060) weekly depth of eight ephemeral, groundwater-driven sinkhole wetlands, Ocala National Forest, Putnam and Marion Counties, Florida, using hydrology models under the CSIRO Mk3.5-A1B climate change scenario

projections; these differences and uncertainties can be magnified when focusing on localized areas. A typical GCM resolution is around 2° latitude/longitude. At this coarse resolution, Florida is basically nonexistent and the area where Florida should be is ocean to the model. The late spring and summer precipitation in the observed data is primarily due to thunderstorms generated along a sea breeze front driven by the land-sea temperature contrast; a process completely absent in the CSIRO Mk3.5 GCM and other GCMs in this location due to the resolution. This leaves the downscaling process as the only method of introducing these local details into climate projections.

Precipitation forecasts under the CSIRO Mk3.5 GCM and A1B emissions scenario, used with our wetland hydrology models resulted in relatively frequent, short-duration hydroperiods at most wetlands for several decades that would likely enhance reproduction and recruitment opportunities for *S. holbrookii*, but result in decreased recruitment opportunities, reduced populations, or possible local extinction of the other four anuran species tested. Even minimal hydroperiod requirements for *A. quercicus*, *A. terrestris*, *L. capito*, and *G. carolinensis* were absent from most wetlands from 2025 to 2035, and optimum hydroperiod requirements were absent from most wetlands through 2042. Best-case forecasts of 11 to 17-year intervals between even minimally suitable hydroperiods (thus no juvenile recruitment) is longer than the estimated 4- to 7-year lifespan of these species (Greenberg 2001; Greenberg and Tanner 2005a, b), increasing the likelihood of their local extinction. Suitable hydroperiods occurring after 2042 may come after these species are already locally extinct. Because our definition of "suitable hydroperiod" was based on a very conservative cutoff for minimum required water depth (≥1 cm), these forecasts present a best-case scenario of suitable hydroperiod frequencies.

Hydroperiod is not the only factor associated with successful anuran breeding and juvenile recruitment from a given wetland. In our study area, both breeding effort and juvenile recruitment of several anuran species are highly variable among years and wetlands, even among wetlands having similar and seemingly suitable hydroperiod characteristics (Greenberg 2001; Greenberg and Tanner 2005a, b). A high frequency of minimum versus optimum forecasted

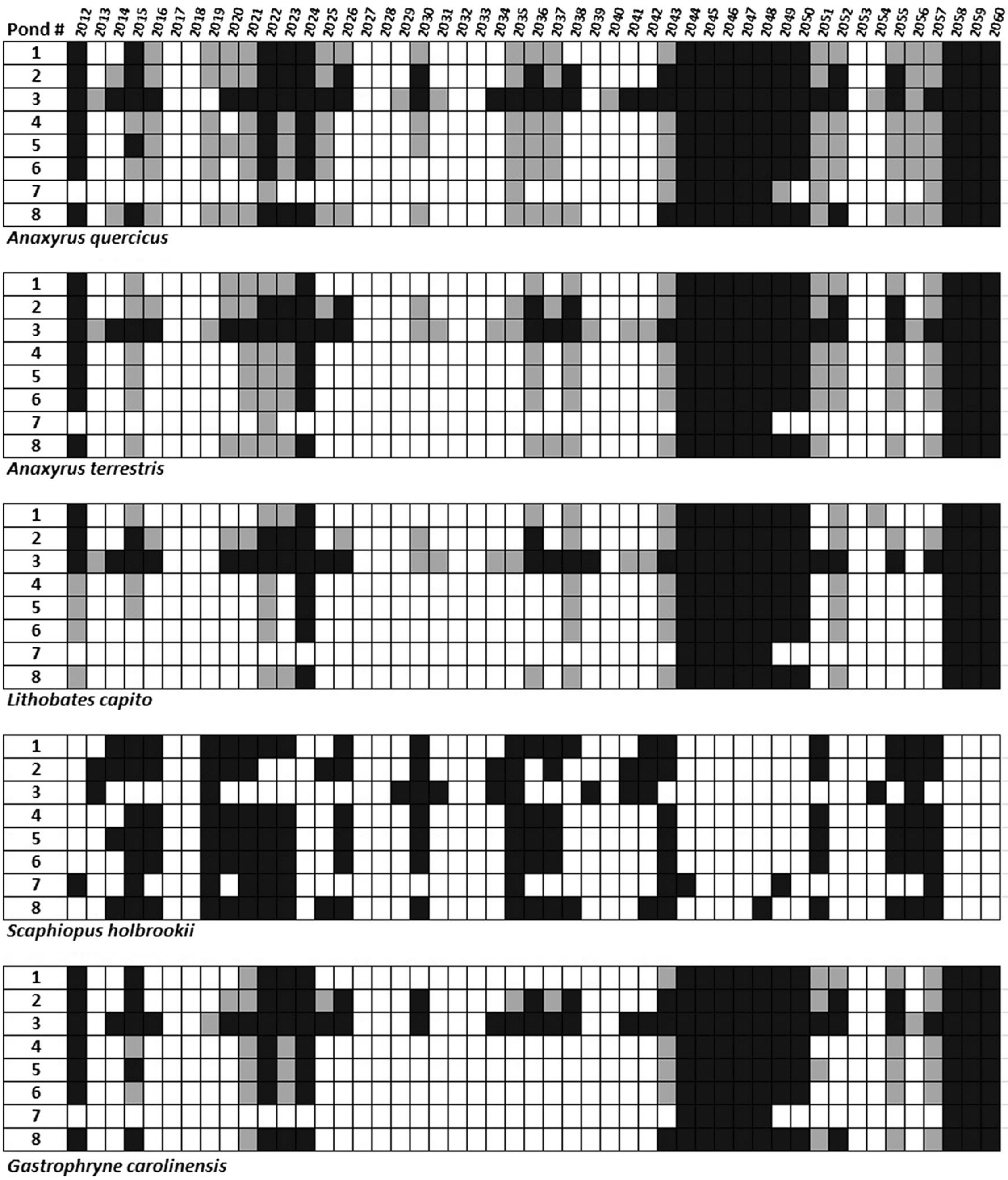

Fig. 7 Years (2012–2060) when minimum (*gray*) and optimum (*black*) timing and duration of hydroperiod (≥1 cm depth) is forecast to be met for five anuran species (*Anaxyrus quercicus*, *A. terrestris*, *Gastrophryne carolinensis, Lithobates capito*, and *Scaphiopus holbrookii*) at eight ephemeral, groundwater-driven sinkhole wetlands under the CSIRO Mk3.5-A1B climate change scenario

hydroperiods, in combination with seemingly stochastic recruitment outcomes even under suitable hydroperiod conditions, further reduces the likelihood of sustained populations of most anuran species that depend primarily on small ephemeral wetlands, under this scenario.

Various changes to hydroregime, such as those we illustrated using the CSIRO Mk3.5 GCM with the A1B emissions scenario, could affect biological diversity and metapopulations at the landscape level by impacting inter-wetland movements, recruitment, recolonization and genetic exchange (Brooks 2009) for many species in addition to the five we used as examples. Long-term drying of a large proportion of wetlands (e.g., 2025–2042 under a CSIRO Mk3.5-A1B scenario) could reduce dispersion among wetlands and increase isolation of primarily-aquatic species such as cricket frogs (*Acris gryllus*), pig frogs (*L. gryllio*), swamp snakes (*Seminatrix pygaea*), and aquatic turtles that do not persist at wetlands that are dry for multiple sequential seasons. Many amphibian species that inhabit uplands as adults, but use wetlands for breeding also could decline or become locally extinct following multiple, sequential years of dry wetlands within a landscape (e.g., Walls et al. 2013b). Repopulation and genetic exchange would depend on sustained successful recruitment at a small proportion of wetlands with sufficiently frequent suitable hydroperiods (e.g., wetlands 2 and 3 in our examples; Fig. 7), and distances between wetlands that were not prohibitively great to allow individuals to recolonize and successfully breed in suitable wetlands that that were previously dry for multiple years.

In our models, temperature was not a significant factor in predicting hydroperiods for ephemeral, groundwater-driven sinkhole wetlands. Nonetheless, amphibian breeding phenology, and larval survival and developmental rates are influenced by both temperature (e.g., Blaustein et al. 2001, 2010; Corn 2005; Todd et al. 2011) and precipitation (see Greenberg et al. 2014). Many amphibian species rely on specific weather cues such as temperature (e.g., Beebee 1995; Saenz et al. 2006; Todd et al. 2011) and precipitation (Corn 2005; Greenberg and Tanner 2005a) to trigger breeding activity. Thus, our estimates of suitable timing and duration of hydroperiods for different species could be mediated by potential future changes in temperature and its influence on breeding ecology for different species.

Our hydrological models, used with downscaled climate data, can be used by land managers and planners to compare potential future changes in hydroregimes at ephemeral, groundwater-driven sinkhole wetlands, and illustrate how breeding success, populations, and relative abundance of select wetland-dependent species could be affected by climate change. Life history attributes such as the timing and length of breeding seasons, breeding cues, rates of larval development to metamorphosis, dispersal ability, and longevity would likely be important mediators of amphibian population trends, relative abundance, and extinction risks among species. Uncertainties associated with predicting climate change and associated weather scenarios magnify the conservation value of retaining multiple ephemeral wetlands with variable frequency, duration, and seasonal timing of hydroperiods. Retention of multiple wetlands will maximize the potential availability of suitable sites for successful reproduction by different species and provide population sources for recolonization at the landscape level.

Acknowledgments Funding was provided by the USDA Forest Service Ocala National Forest; Longleaf Pine Ecosystem Restoration Program; Southern Research Station; Southern Region (R8); Department of Energy-Savannah River Operations (IA Agreement DE-AI09-76SR00056); and the Florida Fish and Wildlife Conservation Commission (contracts NG99-014 and C1195). We thank J. Beach, S. Wazny, D. Wooten, R. Ashton, M. Welker, J. Smith, J. Staiger, J. Barichivich, R. Owen, D. Johnson, S. Johnson, J. Wiebe, K. Garren, E. Roznik, T. Sheltra, R. Ashton, S. Doucette-Riisse, C.J. Kovach, C. Bugbee, R. Lara, L. Tirado, and I. Luque for fieldwork. We also thank L. Lowery, R. Lowery, C. Sekerak, J. Hinchee, J. Clutts, J. Marr, M. Clere, M. Herrin, and the fire crew for assistance. We thank several anonymous reviewers and the Associate Editor for *Wetlands* for their helpful suggestions.

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