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ORIGINAL RESEARCH

Drying Rates of Ephemeral Wetlands: Implications for Breeding Amphibians

Houston C. Chandler[1,2] · **Daniel L. McLaughlin**[3] · **Thomas A. Gorman**[1,4] · **Kevin J. McGuire**[3,5] · **Jeffrey B. Feaga**[1] · **Carola A. Haas**[1]

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Abstract Ephemeral wetlands provide breeding habitat for many amphibian species, and wetland hydrology plays a crucial role in determining amphibian breeding success. We discuss the potential influence of recession rates (i.e., rate of water level decline) and empirically evaluate them in wetlands inhabited by the endangered reticulated flatwoods salamander (*Ambystoma bishopi*). Rapid water level declines are potentially problematic for reticulated flatwoods salamanders because this species has a long development period, with metamorphosis generally occurring from March to May when groundwater losses are combined with high evapotranspiration rates. To evaluate magnitude, variability, and drivers of recession rates, we monitored water levels in 33 wetlands in the Florida panhandle and examined recession rates during the flatwoods salamander reproductive period. After controlling for the effects of specific yield, standardized recession rates were, on average, 3.9 times daily potential evapotranspiration rates, suggesting that groundwater fluxes are an important driver of water level declines in these wetlands. Standardized recession rates were variable across the landscape and increased with decreasing wetland size, indicating that larger wetlands are often hydrologically more suitable for flatwoods salamanders. This work points to these and other controls on wetland recession rates and their role in regulating amphibian reproductive success.

Keywords *Ambystoma bishopi* · Reticulated flatwoods salamander · Florida · Hydrology · Pine flatwoods · Recession rates

Introduction

Ephemeral wetlands of the southeastern United States support a high diversity of breeding amphibians (Russell et al. 2002; Gibbons et al. 2006; Erwin et al. 2016), partly due to wetland hydrologic regime, which supports reproduction while limiting predation (Skelly 1997). Such wetlands include pine flatwoods wetlands, Carolina bays, cypress domes, and karst ponds. Wetlands typically fill for 4–9 months a year with marked variability in hydroperiod (i.e., flooding duration) within and across systems (Sutter and Kral 1994; Sharitz 2003; Chandler et al. 2016). Moreover, these wetland types are often geographically isolated (completely surrounded by uplands) and typically have limited connections to other water bodies (Tiner 2003). As such, ephemeral wetlands typically do not support populations of fish and other predators that require aquatic dispersal connections to and from such water bodies, reducing the risk of egg and larval depredation for breeding amphibians (Skelly 1997; Whiles and Goldowitz 2001; Holbrook and Dorn 2016). However, ephemeral-

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✉ Houston C. Chandler
houstonc@vt.edu

[1] Department of Fish and Wildlife Conservation, Virginia Tech, 100 Cheatham Hall, 310 West Campus Dr., Blacksburg, VA 24061, USA

[2] Present address: The Orianne Society, 11 Old Fruitstand Lane, Tiger, GA 30576, USA

[3] Department of Forest Resources and Environmental Conservation, Virginia Tech, 313 Cheatham Hall, 310 West Campus Dr., Blacksburg, VA 24061, USA

[4] Present address: Aquatic Resources Division, Washington State Department of Natural Resources, Chehalis, WA 98532, USA

[5] Virginia Water Resources Research Center, Virginia Tech, 210 Cheatham Hall, 310 West Campus Dr., Blacksburg, VA 24061, USA

wetland breeding amphibians risk complete reproductive failure if wetlands dry before larvae can develop, metamorphose, and emerge on land, making hydrologic regime a critical driver of population viability (Taylor et al. 2006; Chandler et al. 2016).

Previous studies have emphasized the importance of hydroperiod to amphibian diversity and reproductive success (e.g., Pechmann et al. 1989; Snodgrass et al. 2000; Semlitsch 2002; Baldwin et al. 2006), with boom and bust cycles in reproduction often linked to shifts in hydroperiod (Semlitsch et al. 1996). However, hydroperiod is not the only characteristic of hydrologic regime that potentially influences amphibian reproductive success, as the length of the larval period and time until metamorphosis for many amphibians is plastic and responsive to environmental conditions (Wilbur and Collins 1973; Semlitsch and Wilbur 1988). Recession rate, or rate of declining water levels, is likely important in two major ways — first in controlling access to high quality larval habitat for growth (Fig. 1a) and second for its role in triggering metamorphic transition. Many amphibian larvae use shallow aquatic habitats with dense emergent herbaceous vegetation that occur at the transition zone of upland and wetland plants (i.e., ecotone), where foraging opportunities are high and predation risks may be lower (Baber and Babbitt 2004; Egan and Paton 2004; Porej and Hetherington 2005; Hartel et al. 2007; Gorman and Haas 2011; Chandler et al. 2015). After a wetland is filled, the recession rate regulates the spatial extent and duration that this habitat is inundated (Fig. 1a).

Second, recession rate also has implications for the ability of amphibian larvae to initiate and complete metamorphosis. Metamorphosis is triggered by factors that are related to increased larval mortality risk or declining growth rate, such as crowding, reduced food availability, rising or variable temperature, and/or increased exposure to predators (e.g., Wilbur and Collins 1973; Werner 1986; Morey and Reznick 2000; Gomez-Mestre et al. 2013). These factors or cues are often a consequence of declining water levels and wetland drying rates (Semlitsch and Wilbur 1988; Gomez-Mestre et al. 2013). The process of metamorphosis can take several days, requiring equal or longer time periods between cues (e.g., crowding or increased temperature) that initiate metamorphosis and complete wetland drying (Fig. 1a). Given the influences on habitat availability, as well as triggering and completion of metamorphosis, the recession rate of wetland water levels may be as important as hydroperiod for amphibian reproductive success.

Principal drivers of wetland recession rates include water fluxes and the role of wetland bathymetry (i.e., basin topography) in determining how fluxes induce changes in wetland water levels and spatial extent of inundation (Fig. 1b). Ephemeral flatwoods wetlands often have limited surface water connections, making evapotranspiration (ET) and groundwater fluxes the primary controls on recession rates following rain events (Park et al. 2014). Wetland ET is often assumed to be primarily regulated by climatic conditions, with rates near theoretical potential ET (i.e., maximum ET for a given surface under well-watered conditions; Thornthwaite 1948; Lu et al. 2005). However, ET rates can vary across systems because of differences in vegetation type and structure, suggesting an indirect effect of vegetation on wetland hydrology (Mohamed et al. 2012). Compared to ET, groundwater fluxes (inflows and outflows) are typically more variable across and within ephemeral wetlands and are regulated by soil properties and surrounding hydraulic head gradients (e.g., Winter and LaBaugh 2003; Fig. 1b). Despite the variation and importance of ET and groundwater fluxes, they remain challenging to empirically measure across multiple wetlands since most methods require extensive instrumentation and hydrologic property characterization of subsurface materials.

While ET and groundwater fluxes have obvious and direct influences on recession rates, the changes in water levels and spatial extent of flooding that they create are determined by wetland bathymetry. Bathymetry effects are twofold. First, relationships among wetland stage, flooded area, and volume transform fluxes into stage changes, as well as determine the flooded area at each stage (Fig. 1; Park et al. 2014). Second, bathymetry influences stage-dependent specific yield (S_y) values (McLaughlin and Cohen 2014; Hill and Durchholz 2015). S_y (also called drainage porosity) is the ratio of inflow or outflow depth (e.g., depth of rain or ET) to the resulting water level change. Values equal to 1.0 mean that water depth changes equal the input/output rate (e.g., 5 mm water level change due to 5 mm of precipitation); values less than 1.0 result in higher water level responses (e.g., 25 mm change due to 5 mm of precipitation, with $Sy = 0.2$) (Healy and Cook 2002; Hiscock and Bense 2014). S_y is commonly assumed to be equal to 1.0 in flooded systems (Mitsch and Gosselink 2007; Hill and Neary 2007). However, rapid equilibration between water levels in inundated and non-inundated wetland areas can result in reduced wetland S_y at low stage (McLaughlin and Cohen 2014; Hill and Durchholz 2015). In this case, a given outflow rate will result in greater water level declines at low stage ($S_y < 1.0$) than at high stages ($S_y \sim 1.0$), underscoring the need to account for stage-dependent S_y values when interpreting fluxes from water level change. However, methods to construct site-specific relationships between stage and S_y require extensive datasets (McLaughlin and Cohen 2014; Hill and Durchholz 2015).

Here, we evaluate the magnitude, variability, and drivers of wetland recession rates and then discuss how they could influence ephemeral wetland-breeding amphibians of the southeastern Coastal Plain, particularly reticulated flatwoods salamanders (*Ambystoma bishopi*). However, the requisite instrumentation and datasets necessary to measure water fluxes and wetland S_y make it difficult to separately quantify the roles of ET, groundwater flows, and bathymetry on recession rates across multiple sites (Fig. 1b). With this in mind, we present an approach using time series of wetland water levels to

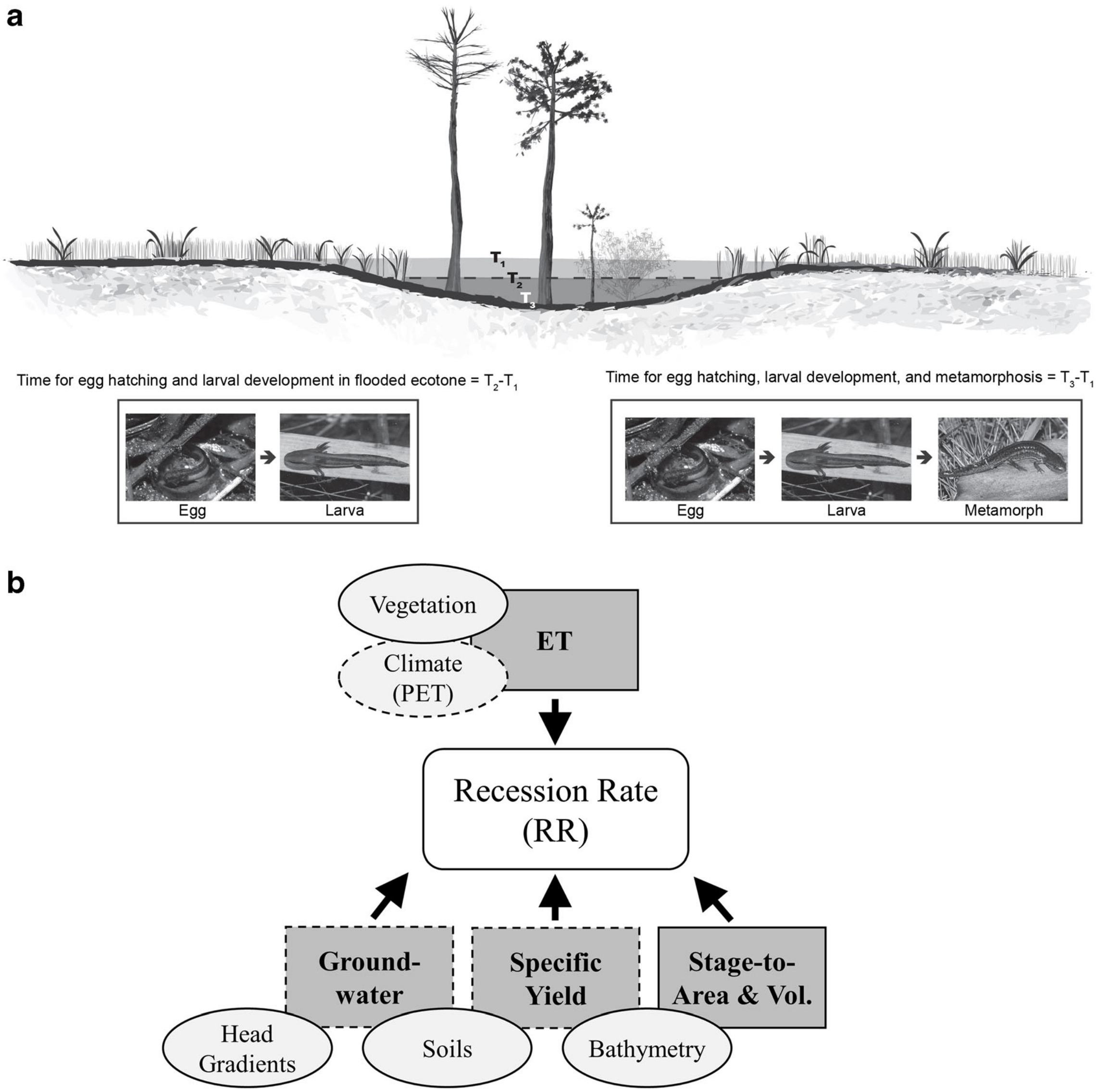

Fig. 1 Cross section of a pine flatwoods wetland indicating how wetland flooding impacts the extent of available habitat for breeding reticulated flatwoods salamanders (*Ambystoma bishopi*) (**a**). Time 1 (T_1) represents the water level after the wetland has completely flooded, allowing access to high-quality ecotone habitat. Time 2 (T_2) represents the water level at which high-quality ecotone habitat is no longer flooded, but salamanders still have time to complete metamorphosis. The difference between T_2 and T_1 represents the time that larval salamanders have access to high-quality ecotone habitat. Time 3 (T_3) indicates the point at which the wetland has dried and larval salamanders must have metamorphosed. A conceptual diagram indicating the climatic and site-specific drivers that influence recession rates (i.e., rate of declining water level) of an ephemeral wetland (**b**). *Dashed lines* indicate aspects of recession rate that we addressed in this manuscript

account for the influence of two hydrologic drivers (climate and S_y) on recession rates, allowing us to infer relative magnitudes of groundwater fluxes across 33 flatwoods wetlands in north Florida. Our objectives were to: 1) estimate the relative contribution of groundwater fluxes to recession rates across systems; 2) explore controls on groundwater fluxes in flatwoods wetlands; and 3) identify future work to fully elucidate influences and drivers of recession rates and to inform targeted restoration and conservation efforts for flatwoods salamander populations.

Methods

Study Sites

We monitored water levels in 33 pine flatwoods wetlands located on Eglin Air Force Base (AFB) in Okaloosa and Santa Rosa counties, Florida. Eglin AFB is a large military installation covering over 187,000 ha, of which a majority is actively managed longleaf pine (*Pinus palustris*) forests. Wetlands were located in three different study areas (with the soil types of each shown in parentheses): East Bay Flatwoods (primarily Chipley [Aquic Quartzipsamments], Leon [Aeric Alaquods], and Rutlege soils [Typic Humaquepts]), Oglesby's Flatwoods (primarily Chipley, Leon, and Rutlege soils), and Whitmier Island Flatwoods (primarily Johns [Aquic Hapludults] and Pactolus [Aquic Quartzipsamments] soils). These soils range from sandy to sandy loam textures with moderate to high hydraulic conductivities (Soil Survey Staff 2016). In general, the hydrology of the depressional wetlands in the area is poorly studied. Wetlands are usually full from winter to early spring when ET rates are low and then experience a fairly constant dry period during summer months when ET rates are high (Chandler et al. 2016). The 33 wetlands included in our study were part of existing amphibian monitoring and restoration projects and were originally selected for inclusion in these projects based on their vegetation characteristics (see Gorman et al. 2013).

Pine flatwoods wetlands are part of the fire-maintained longleaf pine ecosystem. Flatwoods wetlands are characterized by open savannas of longleaf pine and wiregrass (*Aristida stricta*, *A. palustris*) with diverse forbs throughout most of the shallow basin, often containing slash pine (*Pinus elliottii*) or pond cypress (*Taxodium ascendens*) in basin centers. A recent (80–90 year) history of fire exclusion and suppression in longleaf pine ecosystems has resulted in wetlands historically used for breeding by flatwoods salamanders becoming overgrown with a dense midstory of woody shrubs, which reduces breeding habitat quality (Kirkman 1995; Bishop and Haas 2005; Gorman et al. 2009; Martin and Kirkman 2009). Work is currently ongoing at Eglin AFB to restore habitat for reticulated flatwoods salamanders (e.g., Gorman et al. 2013), an endangered species, based on vegetative descriptions of occupied wetlands (Palis 1997; Sekerak et al. 1996; Gorman et al. 2009). In addition to flatwoods salamanders, these wetlands provide habitat for at least 16 other species of amphibians, the majority of which breed in these wetlands (Chandler et al. 2015).

Reticulated Flatwoods Salamanders

Reticulated flatwoods salamanders are native to the southeastern Coastal Plain, and have experienced severe population declines, primarily due to habitat loss and degradation (USFWS 2009). Flatwoods salamanders have an unusual reproductive strategy that is tightly linked with wetland hydrology. During the fall (October–December), flatwoods salamanders deposit eggs in dry wetlands, typically in ecotone areas with high density of herbaceous vegetation (Anderson and Williamson 1976; Hill 2013; Gorman et al. 2014). Eggs hatch (November–February) if ecotones are inundated by fall or winter rains, and larvae typically remain and develop in these flooded ecotone habitats (Sekerak et al. 1996; Gorman et al. 2009), where prey abundance is high (Chandler et al. 2015). Recession rates determine the flooding duration in wetland ecotones, where larvae feed and grow for approximately 3–4 months. Metamorphosis typically occurs from mid-March to late May and can take ca. 10 days from start to finish (Palis 1997).

Data Collection

We installed monitoring wells at an approximate center point in each wetland to monitor water levels from August 2012 to January 2015. We used 3.8 cm diameter, screened PVC pipe and installed wells 1 m below ground. HOBO® U20 pressure transducers (Onset Computer Corporation, Bourne, MA) were deployed in each well to record total pressure at 15 min intervals. Data were corrected for barometric pressure variation (via U20 logger in well head space) and converted to water levels (relative to ground surface). We also installed a HOBO® Data Logging Rain Gauge RG3-M near three wetlands.

For all analyses, we truncated data to only include measurements from October to June, which is the time period that is most relevant to flatwoods salamander breeding and larval development. Daily recession rates (RR) for each wetland were determined as a midnight to midnight water level change, where midnight water levels were mean levels between 23:00 and 1:00. We only calculated daily recessions for periods that occurred at least 48 h after water level increases from precipitation events had subsided. Because we were interested in how drying rates affected amphibian breeding potential, we also removed all daily recessions that occurred when water levels were below ground.

Finally, we standardized all RR with daily potential ET (PET) to account for temporal climatic variability and its effect on ET rates. Standardized daily recession rates (RR/PET) are unitless values. PET data were downloaded from three Florida Automated Weather Network (FAWN; http://fawn.ifas.ufl.edu/) stations in northwest Florida (Jay, Marianna, and DeFuniak Springs), and the closest weather station to the study sites was always used when data were available (three weather stations were necessary because of occasional data gaps). We then calculated average RR/PET for each wetland over the time period of analysis. Note that daily PET used here is calculated with the FAO Penman-Monteith method for a well-watered reference grass (Allen et al. 1998), accounting for variability in climate but not surface roughness and resistance (e.g., vegetation structure). Indeed, most empirically-based methods estimate PET solely using climate data (Drexler et al. 2004; Lu et al. 2005), with some exceptions (e.g., Monteith 1965). Hereafter, we consider PET as estimated evaporative demand of the atmosphere, thereby accounting for climatic but not vegetation variation across sites and time.

Rapid equilibration of water levels between flooded and exposed wetland areas can cause $S_y < 1$ at lower stages, resulting in amplified water level changes to a given flux. To account for this effect, we plotted daily RR/PET against wetland water level to identify potential influences of S_y at low stages. We performed a piece-wise regression to identify points where the slope of a best fit line significantly changed from zero (i.e., systematic increase in RR/PET with decreasing stage because of lower S_y). For each wetland, we removed RR/PET values occurring at or below this stage threshold of marked S_y influence. With these data, we then calculated another average RR/PET for each wetland to represent values excluding S_y influences (RR_{-Sy}/PET). Comparing RR/PET and RR_{-Sy}/PET (rates before and after removing S_y influences) allowed us to explore the effect of S_y on recession rates for each wetland. Further, resulting RR_{-Sy}/PET values reflect ratios of daily decline (ET plus groundwater fluxes) relative to PET, allowing us to compare net magnitude of fluxes after excluding effects of climatic variability and S_y. Lastly, assuming that ET is approximately equivalent to PET (under flooded, well-watered conditions) allowed us to infer and compare relative contributions of groundwater fluxes on recession rates across the 33 wetland sites.

To explore potential drivers of RR_{-Sy}/PET, we measured several biotic and abiotic wetland attributes including wetland vegetation characteristics (canopy and herbaceous vegetation cover), wetland area, and elevation of wetland ground surface (at well). We measured canopy cover at multiple points (≥7, number of points was scaled to wetland size) in each wetland using a convex spherical densiometer and then averaged measurements to create a canopy cover estimate for the entire wetland (canopy cover estimates included vegetation from the overstory and midstory). We also measured percent herbaceous vegetation cover at the same points using a Daubenmire (1959) frame. We averaged all herbaceous vegetation cover measurements to create an estimate of total cover in each wetland. We estimated maximum wetted area at full maximum stage of each wetland using GPS and calculated the ground elevation at each monitoring well using LIDAR data (Jackson Guard, Eglin AFB) from our study area.

Statistical Analyses

We examined the effects of vegetation (canopy and herbaceous vegetation cover), wetland area (log transformed), and wetland elevation on RR_{-Sy}/PET using simple linear regression models (three models total). We applied a logarithmic transformation to wetland area to increase the linearity in this relationship. We examined the effect of wetland location (i.e., the three study areas) using an ANOVA and used Tukey's HSD to perform post hoc multiple comparisons. All analyses were performed in R (R Core Team 2014), using the packages 'xts' and 'zoo' for time series data (Ryan and Ulrich 2014; Zeileis et al. 2015) and using the package 'segmented' for piece-wise regressions (Muggeo 2015).

Results

Over the 3.5-year period, average wetland water levels during the flatwoods salamander breeding season ranged across sites from 5.5 ± 2.7 to 38.8 ± 25.3 cm (mean ± SD), reflecting the variability among and within wetlands. There was temporal variability in water levels both between and within years. For example, the 2012–2013 flatwoods salamander breeding season was characterized by drought (mean water level across all wetlands ~ 15 cm below ground), whereas the 2013–2014 breeding season was characterized by above average precipitation (mean water level ~19 cm above ground). Most wetlands experienced flooded and non-flooded conditions within each salamander breeding season. As expected, wetlands were most likely to have surface water during the winter and early spring, typically followed by dry periods during the summer months (Fig. 2).

Average RR/PET was variable among wetlands and ranged from 2.80 ± 2.17 to 7.39 ± 4.46 (mean ± SD; Table 1; Fig. 3). Recession rates were influenced by S_y at low stages in 19 of 33 wetlands (Table 1; dashed lines in Fig. 4a and b). There was substantial variation in threshold stage values (slope breakpoint in Table 1) at which this effect occurred and in the effect magnitude (i.e., slope). Threshold stage values ranged from 5.2 to 37.3 cm, and slope for best fit lines over the S_y-influenced area ranged from −0.07 to −2.38 (Table 1). For these 19 wetlands, removing data with S_y influence decreased mean recession rates and resulted in RR_{-Sy}/PET values more similar (e.g., SD in mean RR/PET = 1.37 vs. SD in mean RR_{-Sy}/PET = 0.97 without S_y influence) across sites (Table 1; Fig. 5). Comparing ranks of sites using RR/PET vs. RR_{-Sy}/PET highlights the site-varying influence of S_y on wetland water level fluctuations. Accounting for this S_y effect, RR_{-Sy}/PET values were still higher than one across all wetlands (Range: 2.80 ± 2.17 to 6.57 ± 3.24 [mean ± SD]), meaning that a substantial portion of daily decline was due to groundwater fluxes (assuming that ET ~ PET). As such, values approximate the relative contribution of groundwater fluxes to recession rates (e.g., RR_{-Sy}/PET = 4.0 implies ca. 80% of mean daily decline is due to groundwater losses, with the other ~20% due to ET). With this interpretation, RR_{-Sy}/PET values point to large differences in groundwater fluxes across sites and marked temporal variability within sites (Table 1, Fig. 5).

There was a significant effect of wetland location on RR_{-Sy}/PET ($F_{2,30} = 4.5$, $P = 0.02$), with wetlands in the Whitmier Island Flatwoods having higher RR_{-Sy}/PET than wetlands in the East Bay Flatwoods ($P = 0.014$). However, neither the percent canopy cover ($t = -1.32$, $P = 0.20$) nor the percent herbaceous vegetation cover ($t = -0.08$, $P = 0.94$) within a wetland had an effect on RR_{-Sy}/PET. Wetland area had a strong negative effect on RR_{-Sy}/PET ($t = -4.73$, $P < 0.001$). Finally, wetland elevation had no effect on RR_{-Sy}/PET ($t = -1.39$, $P = 0.17$).

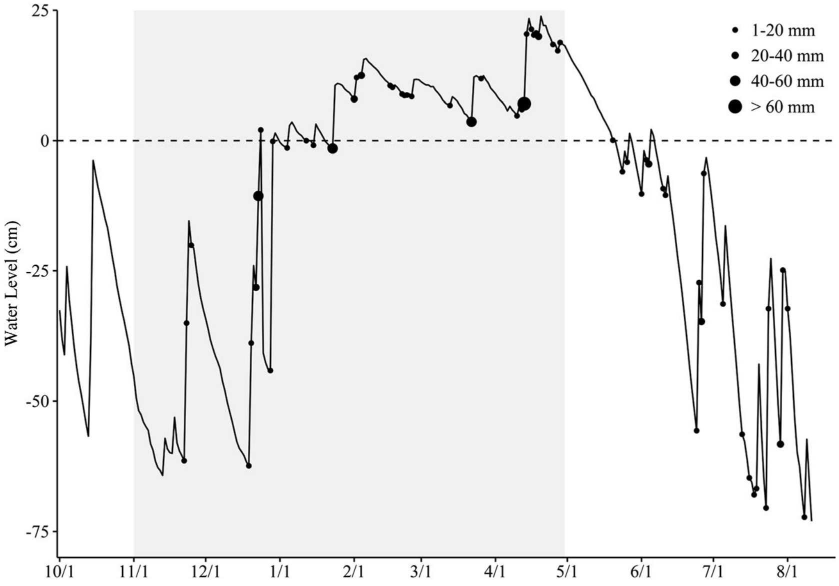

Fig. 2 Water levels for a pine flatwoods wetland located on Eglin Air Force Base, Florida from October 2014 to August 2015. *Circles* represent precipitation events (data were only available beginning in late November). The shaded area represents the time period that is most important for flatwoods salamander reproduction, and the *dashed grey line* separates surface and subsurface water levels

Discussion

The importance of wetland hydrologic regime — not only hydroperiod but also flooding location and rate of water level change — on amphibian reproduction underscores the need to elucidate and quantify the drivers of recession rates (Fig. 1). Our approach allowed us to effectively examine recession rates in 33 pine flatwoods wetlands and assess the relative contributions of groundwater fluxes to daily water level declines, while controlling for other hydrologic factors (e.g., S_y and ET). Furthermore, we were able to examine the influence of several biotic and abiotic factors on recession rates and inferred groundwater fluxes, providing useful information to guide wetland restoration strategies and target conservation efforts for flatwoods salamanders.

Understanding the drivers of recession rates and its variation across sites can inform management efforts that target locations with suitable hydrology to increase or repatriate populations of flatwood salamanders. After correcting for the effects of S_y at low stages, we documented recession rates that were, on average, almost four times the daily PET rate. Such values for RR_{-Sy}/PET, even when considering plausible differences between actual ET and estimated PET rates (<30% in similar Florida wetland systems; McLaughlin and Cohen 2013), indicate that drying rates in studied pine flatwoods wetlands are largely due to net groundwater losses. Geographically isolated wetlands can have variable groundwater interactions depending on a variety of factors including topography, upland water table depths, soil properties, and vegetative conditions (Hayashi and Rosenberry 2002; Lu et al. 2009). Previous research in cypress swamps in pine flatwoods of north Florida found that wetland groundwater fluxes switch between inflow and outflow in response to rain events, but that groundwater outflow was dominant and consistent during sustained wetland drying (Riekerk and Korhnak 2000; McLaughlin and Cohen 2013).

Wetlands included in this study varied in wetted area (0.13–5.92 ha), making it important to investigate the effects of wetland area on hydrologic processes. Wetland area was the best predictor of RR_{-Sy}/PET values, with larger wetlands having significantly lower values than smaller wetlands. For example, wetlands under 1 ha had an average RR_{-Sy}/PET of 4.6 ± 0.3 (SE, $n = 15$), while wetlands over 2 ha had an average RR_{-Sy}/PET of 3.3 ± 0.1 (SE, $n = 8$). Furthermore, wetlands that were occupied ($n = 8$) by flatwoods salamanders at least once between 2008 and 2015 were larger than non-occupied ($n = 25$) wetlands ($t = 2.52$, $P = 0.008$) (Haas and Gorman, unpublished data). Wetland area also had a positive effect on wetland hydroperiod at some of the same pine flatwoods wetlands (Chandler et al. 2016). Together, these results indicate that larger wetlands are likely more hydrologically suitable for the long larval periods characteristic of flatwoods salamanders (Palis 1997). However, larger wetlands that are more likely to be inundated and have slower recession rates are also less likely to burn during prescribed fires (Kirkman 1995; Bishop and Haas 2005). Thus, these wetlands may be more likely than smaller wetlands to develop vegetation structures characteristic of fire suppression and exclusion (i.e., a thick woody midstory and declining herbaceous vegetation). These vegetation changes can have negative effects (e.g., less invertebrate prey abundance; Chandler et al. 2015) on flatwoods salamanders and other breeding amphibians and may offset some of the hydrologic benefits of breeding in larger wetlands (Gorman et al. 2009; Gorman et al. 2013). Consequently, restoration efforts to improve herbaceous cover (e.g., prescribed fires within wetlands) may be most effective in larger wetlands with these lower recession rates.

Table 1 Average recession rates for 33 pine flatwoods wetlands located on Eglin Air Force Base, Florida

Wetland ID	RR/PET	Rank	S_y Point	S_y Slope	RR/PET_{-Sy}	Rank without S_y	Ever FS	Recent FS
34	2.80 (± 2.17)	1			2.80 (± 2.17)	1	X	X
50	2.98 (± 2.29)	2			2.98 (± 2.29)	2		
53	3.10 (± 1.86)	3			3.10 (± 1.86)	5	X	X
103	3.12 (± 2.45)	4			3.12 (± 2.45)	6		
15	3.19 (± 2.68)	5			3.19 (± 2.68)	7	X	X
111	3.32 (± 2.73)	6			3.32 (± 2.73)	10		
107	3.39 (± 2.33)	7			3.39 (± 2.33)	11		
19	3.40 (± 2.47)	8			3.40 (± 2.47)	12	X	X
31	3.46 (± 2.80)	9	9.28	−0.58	3.09 (± 2.34)	4		
12	3.48 (± 2.69)	10			3.48 (± 2.69)	15	X	
16	3.48 (± 2.88)	11			3.48 (± 2.88)	16	X	X
202	3.52 (± 3.14)	12	9.85	−0.79	3.03 (± 2.30)	3		
4	3.64 (± 3.12)	13			3.64 (± 3.12)	19	X	X
30	3.65 (± 2.74)	14	9.61	−0.26	3.26 (± 2.74)	9	X	
40	3.66 (± 2.83)	15	17.91	−0.27	3.49 (± 2.62)	17		
2	3.94 (± 2.61)	16	6.38	−0.87	3.56 (± 2.21)	18	X	
201	4.03 (± 3.38)	17	15.90	−0.28	3.20 (± 2.72)	8		
121	4.35 (± 3.87)	18	17.98	−0.45	3.48 (± 2.04)	14		
33	4.37 (± 3.14)	19	5.18	−1.14	3.90 (± 2.17)	21	X	X
72	4.45 (± 2.60)	20			4.45 (± 2.60)	28		
67	4.74 (± 3.45)	21	16.69	−0.32	4.08 (± 2.35)	23		
5	4.89 (± 3.38)	22	9.28	−0.55	4.37 (± 3.12)	27	X	X
3	5.40 (± 4.58)	23	24.68	−0.40	3.81 (± 2.90)	20	X	
200	5.40 (± 4.03)	24			5.40 (± 4.03)	30		
6	5.52 (± 3.48)	25	26.97	−0.08	4.18 (± 3.17)	24		
126	6.04 (± 4.94)	26	6.52	−1.26	4.27 (± 3.24)	26		
51	6.16 (± 3.16)	27			6.16 (± 3.16)	31	X	
1	6.17 (± 5.42)	28	17.96	−0.48	3.43 (± 3.02)	13		
13	6.38 (± 4.07)	29	13.92	−0.57	5.06 (± 2.58)	29	X	
11	6.43 (± 4.10)	30	37.25	−0.07	4.25 (± 2.82)	25		
7	6.63 (± 5.20)	31	26.92	−0.18	3.95 (± 3.05)	22		
69	7.26 (± 4.34)	32	6.92	−2.38	6.57 (± 3.24)	33		
88	7.39 (± 4.46)	33	10.63	−0.59	6.17 (± 2.22)	32		

Recession rates were calculated for every 24-h period (at least 48 h after a precipitation event) between August 2012 and January 2015 and were standardized by daily PET values (RR/PET). Points (S_y point) where recession rates were influenced by specific yield (S_y) were identified, and the slope (S_y slope) of the best-fit line in the S_y influenced region was identified. RR/PET_{-Sy} represents the recession rates after the influence of S_y was excluded. RR/PET and RR/PET_{-Sy} are both ranked from lowest to highest, and standard deviations are presented in parentheses. Wetlands ever (Ever FS) and recently (Recent FS) (2008–2015) occupied by reticulated flatwoods salamanders are also indicated

In addition to the direct effect on habitat structure, vegetation management may also influence recession rates via changes in ET rates. Vegetation differences, particularly leaf area and physiological traits, can often result in different ET rates across similar wetland systems (Sánchez-Carrillo et al. 2004; Mohamed et al. 2012; Orellana et al. 2012). For example, in north Florida cypress domes, ET/PET ranged from 0.77 to 1.34, with values positively correlated with differences in leaf area index (McLaughlin and Cohen 2013). However, we found no effect of wetland vegetation characteristics on recession rates despite high variability in composition and structure across the study sites. The relative contribution of groundwater losses to recession rates (i.e., $RR_{-Sy}/PET >> 1.0$) likely prevented us from identifying any effects of vegetation. That is, variation in groundwater fluxes across systems obscures smaller variation in ET values that may result from differences in vegetation but not climate (i.e., variation in ET/PET). While our inferences of groundwater fluxes assume ET ~ PET, known ranges in ET/PET in systems varying in vegetation structure suggest the potential for vegetation management to influence wetland recession rates.

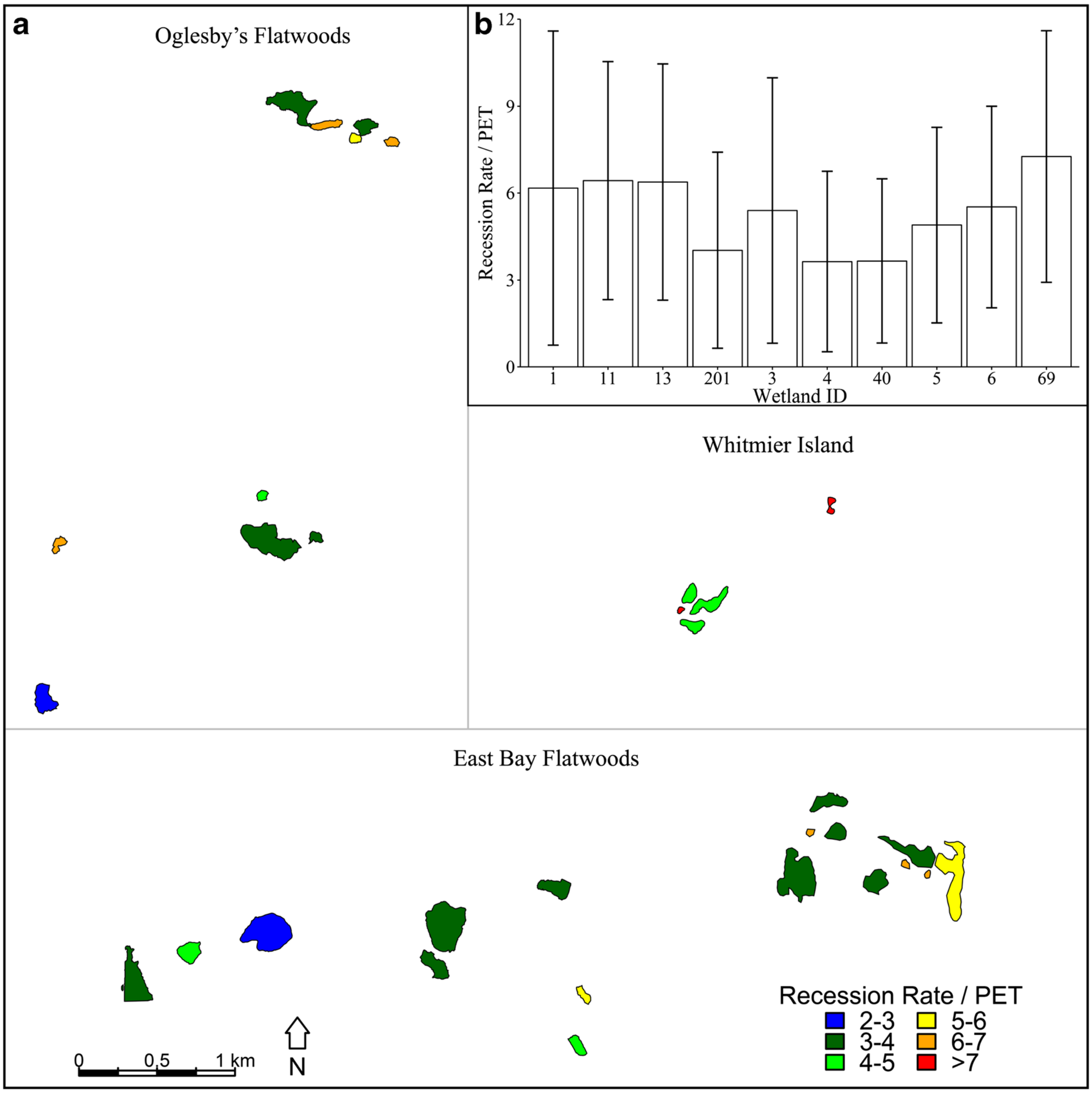

Fig. 3 Average daily recession rates standardized by daily potential evapotranspiration rates (RR/PET) from August 2012 to January 2015 in 32 (one additional wetland is located farther north in East Bay Flatwoods and is not shown here) pine flatwoods wetlands (**a**). RR/PET for 10 of these wetlands are displayed with *error bars* representing standard deviation (**b**). Wetlands were located in three different areas on Eglin Air Force Base, Florida

Wetland basin bathymetry can also influence recession rates via several mechanisms. We detected an effect of S_y on RR/PET in 19 of 33 wetlands, emphasizing the importance of considering this parameter when examining water level fluctuations. After removing the effect of S_y, RR/PET dropped by an average of 20% across the 19 wetlands, with RR/PET in two wetlands decreasing by over 40%. Bathymetry also affects recession rates through stage to area and volume relationships. These relationships determine the change in flooded extent for a given water level decline (with large implications for ecotone habitat availability for larval salamanders, Fig. 1a), but they also determine the water level change induced from a given volumetric flux rate. The latter control means that different RR_{-Sy}/PET values could result from equal groundwater fluxes, possibly explaining the negative correlation between RR_{-Sy}/PET and wetland area. Nonetheless, RR/PET values indicate the degree to which water level decline rates vary across systems; documenting this variation helps in targeting the wetland sizes, bathymetries, and landscape locations most suitable for conservation and restoration efforts.

Understanding landscape drivers (e.g., soils, elevation) of wetland recession rates could have important implications for targeting management actions. Across the three study areas, we found significant differences in recession rates, with the highest rates occurring in Whitmier Island Flatwoods. Although flatwoods salamanders have never been documented in this study area, it has been considered as a potential area

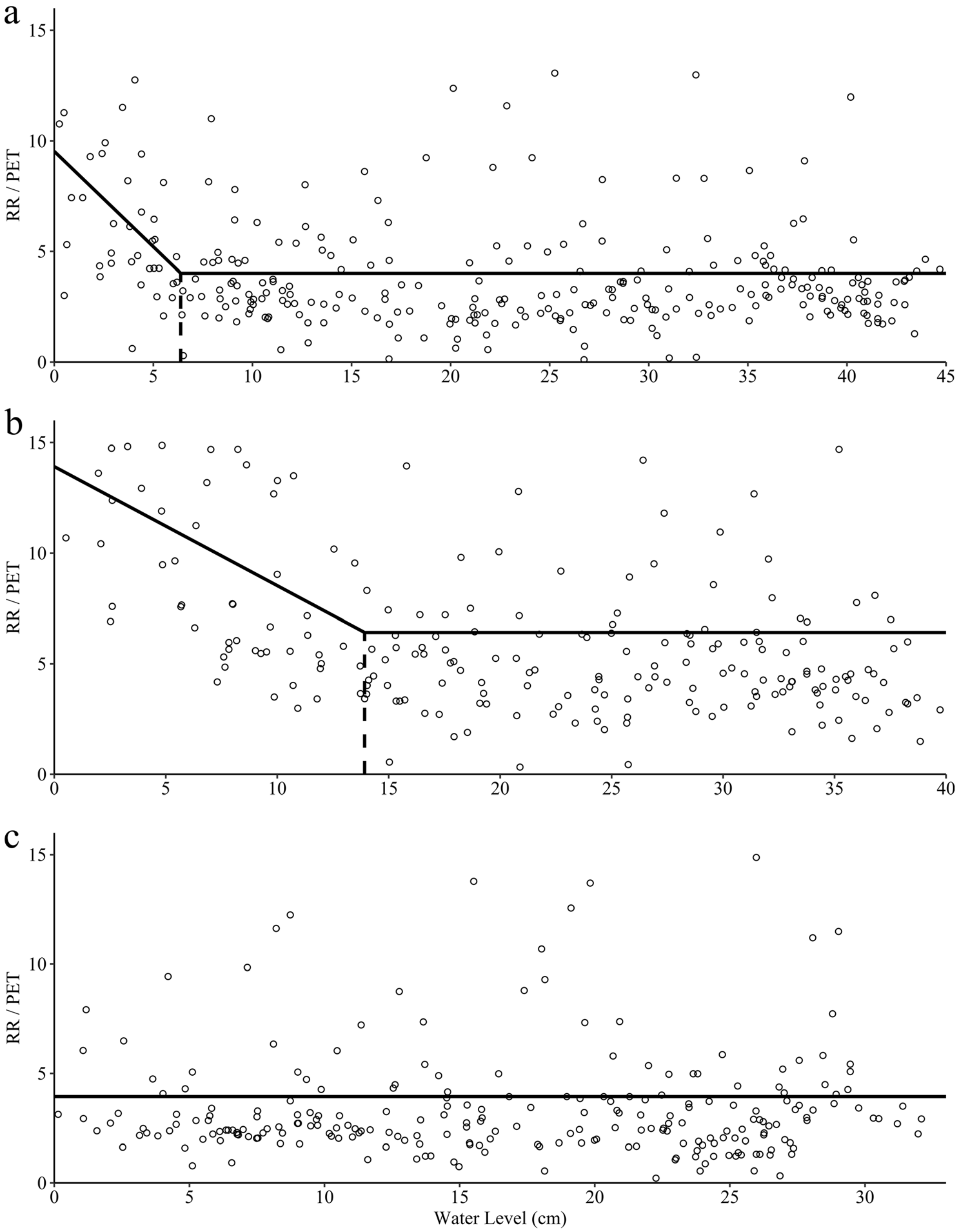

Fig. 4 Daily recession rates standardized by daily potential evapotranspiration rates (RR/PET) vs. water level in three pine flatwoods wetlands (a – Wetland 2; b – Wetland 13; c – Wetland 19) located on Eglin Air Force Base, Florida. Dotted lines represent water levels above which there was no influence of specific yield on recession rates, and solid lines are the best-fit line for each region of data

for translocations, based on vegetative characteristics. However, our results suggest that it may be hydrologically less suitable than other sites. The dominant soil series varied across the three areas, with wetlands in Whitmier Island Flatwoods having primarily Pactolus soils, which have higher hydraulic conductivities (thus potentially more groundwater exchange) compared to the other soil series (Soil Survey Staff 2016). Well elevation (as a potential indicator of head gradients) was also expected to influence recession rates across the landscape, but we found no effect of well elevation. Coupled groundwater and wetland water level monitoring, along with finer-scale soil property characterization, could better identify landscape drivers of wetland drying.

For effective conservation and management of reticulated flatwoods salamanders and other amphibians, it is important to understand the hydrologic processes and habitat conditions that determine suitable breeding wetlands. Ultimately, ideal habitat for flatwoods salamanders would include an extensive ecotone of thick herbaceous vegetation (Gorman et al. 2009) and a hydroperiod of at least 15–18 weeks (the upper distribution of larval development period; Palis 1997) occurring at least 2 years out of five (assuming an adult lifespan of approximately 4–5 years; Palis et al. 2006). Here, our specific focus was on recession rates, which also have critical influences on both larval development and success of metamorphosis. Wetlands with a slow recession rate are most likely to allow

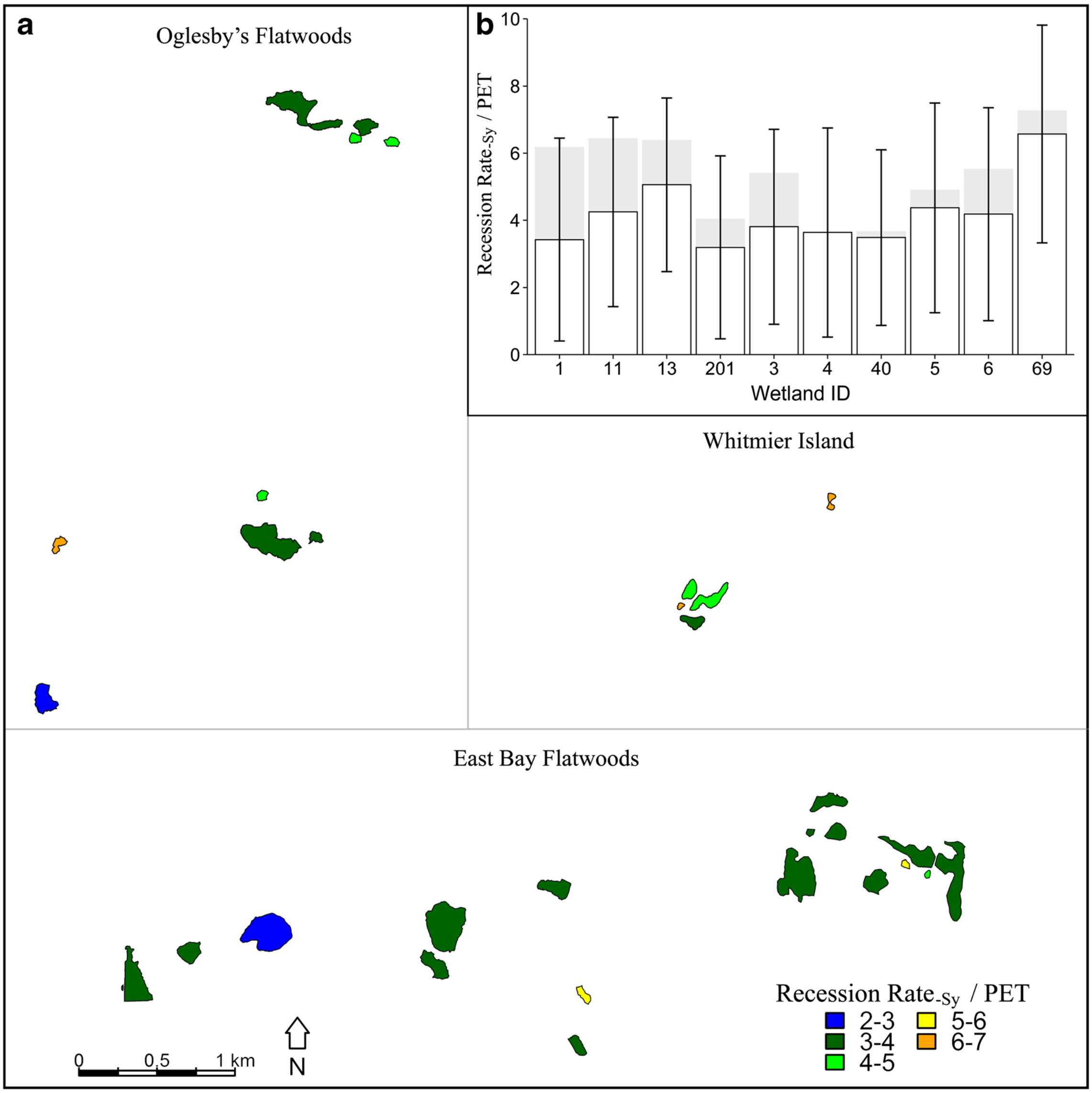

Fig. 5 Average daily recession rates standardized by daily potential evapotranspiration rates with influence of specific yield removed (RR/PET$_{-Sy}$) for 32 (one additional wetland is located farther north in East Bay Flatwoods and is not shown here) pine flatwoods wetlands in three different areas on Eglin Air Force Base, Florida (**a**). RR/PET$_{-Sy}$ for 10 of these wetlands are displayed with error bars representing standard deviation and *grey bars* representing the recession rate prior to removing the effect of specific yield (i.e., RR/PET) (**b**)

larvae to maximize growth rate by using high-quality habitat during much of their development period (Alford and Harris 1988). Larval amphibians that metamorphose at a larger body size have increased adult survival and reproductive success (Scott 1994; Altwegg and Reyer 2003). Finally, for successful flatwoods salamander reproduction, recession rates late in the breeding season (i.e., April–May) need to allow at least 10 days between initiation of metamorphosis and complete wetland drying (Palis 1997). Our work points to groundwater exchange as a major driver of variation in recession rates among wetlands across a landscape, highlighting a key hydrologic process to consider when targeting future translocations of (or land acquisition for) reticulated flatwoods salamanders.

Future Work

The methodology used here allowed us to quantify and compare recession rates across multiple wetlands, but future work is needed to fully explore the suite of hydrologic characteristics important for ephemeral wetland hydrology and its influences on amphibian breeding populations. First, wetland bathymetry, together with wetland vegetation characteristics, plays a crucial role in determining the extent of flooded habitat that is suitable for amphibians (i.e., areas of dense herbaceous vegetation). Measuring the bathymetry of each wetland would directly link stage variation with duration of flooding in a specific habitat. Second, we omitted recession rates occurring at stages with evident influences from S_y. Methods to estimate

S_y as a function of stage exist but require additional data (see McLaughlin and Cohen 2014). Site-specific relationships would convert water level changes to flux rates across all stages, allowing interpretation of rates across entire datasets. Third, we were unable to detect any effects of vegetation structure on recession rates, likely because of the magnitude of groundwater fluxes. However, documented ranges in ET/PET imply that lowering recession rates with reductions in vegetation is plausible, highlighting the need for empirical measures of ET rates in wetlands with varying vegetation management strategies and histories. Measures of leaf area index may also provide a better assessment of wetland vegetation. Lastly, a better understanding of hydrologic processes in flatwoods wetlands will improve predictions of climate change impacts on hydrologic regime and attendant effects on amphibian populations.

In addition to continued investigation of the hydrologic processes that control recession rates in ephemeral wetlands, future work is also needed to quantify effects of recession rates on amphibian population viability. Recession rates either regulate or play an important role in many aspects of larval amphibian ecology, ultimately influencing whether or not larval amphibians can metamorphose before wetlands dry. Future work would ideally focus on the spatial extent and duration of flooded habitat suitable for development of different species, variation in larval growth rates in the different habitat types, and the length of time between hydrologic-driven cues for metamorphosis and complete wetland drying. Empirical evidence of these hydrologically mediated controls on population viability could be coupled with wetland hydrologic monitoring and modeling to design and target species-specific management actions. An integrative understanding of wetland hydrology and species requirements is necessary for effective conservation and management of wetlands and the amphibian species that depend on them.

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References

Alford RA, Harris RN (1988) Effects of larval growth history on anuran metamorphosis. The American Naturalist 131:91–106

Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration – guidelines for computing crop water requirements. FAO irrigation and drainage paper 56. Food and Agriculture Organization of the United States. Rome, Italy

Altwegg R, Reyer H-U (2003) Patterns of natural selection on size at metamorphosis in water frogs. Evolution 57:872–882

Anderson JD, Williamson GK (1976) Terrestrial mode of reproduction in *Ambystoma cingulatum*. Herpetologica 32:214–221

Baber MJ, Babbitt KJ (2004) Influence of habitat complexity on predator-prey interactions between the fish (*Gambusia holbrooki*) and tadpoles of *Hyla squirrela* and *Gastrophryne carolinensis*. Copeia 2004:173–177

Baldwin RF, Calhoun AJK, deMaynadier PG (2006) The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes. Canadian Journal of Zoology 84:1604–1615

Bishop DC, Haas CA (2005) Burning trends and potential negative effects of suppressing wetland fires on flatwoods salamanders. Natural Areas Journal 25:290–294

Chandler HC, Haas CA, Gorman TA (2015) The effects of habitat structure on winter aquatic invertebrate and amphibian communities in pine flatwoods wetlands. Wetlands 35:1201–1211

Chandler HC, Rypel AL, Jiao Y, Haas CA, Gorman TA (2016) Hindcasting historical breeding conditions for an endangered salamander in ephemeral wetlands of the southeastern USA: implications of climate change. PLoS ONE 11:e0150169

Daubenmire RF (1959) A canopy-cover method of vegetational analysis. Northwest Science 33:43–46

Drexler JZ, Snyder RL, Spano D, Paw U, Tha K (2004) A review of models and micrometeorological methods used to estimate wetland evapotranspiration. Hydrological Processes 18:2071–2101

Egan RS, Paton PWC (2004) Within-pond parameters affecting oviposition by wood frogs and spotted salamanders. Wetlands 24:1–13

Erwin KE, Chandler HC, Palis JG, Gorman TA, Haas CA (2016) Herpetofaunal communities in ephemeral wetlands embedded within longleaf pine flatwoods of the Gulf Coastal Plain. Southeastern Naturalist 15:431–447

Gibbons JW, Winne CT, Scott DE, Willson JD, Glaudas X, Andrews KM, Todd BD, Fedewa LA, Wilkinson L, Tsaliagos RN, Harper SJ, Geene JL, Tuberville TD, Metts BS, Dorcas ME, Nestor JP, Young CA, Akre T, Reed RN, Buhlmann KA, Norman J, Croshaw DA, Hagen C, Rothermel BB (2006) Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. Conservation Biology 20:1457–1465

Gomez-Mestre I, Kulkarni S, Buchholz DR (2013) Mechanisms and consequences of developmental acceleration in tadpoles responding to pond drying. PLoS One 8:e84266

Gorman TA, Haas CA (2011) Seasonal microhabitat selection and use of syntopic populations of *Lithobates okaloosae* and *Lithobates clamitans clamitans*. Journal of Herpetology 45:313–318

Gorman TA, Haas CA, Bishop DC (2009) Factors related to occupancy of breeding wetlands by flatwoods salamander larvae. Wetlands 29: 323–329

Gorman TA, Haas CA, Himes JG (2013) Evaluating methods to restore amphibian habitat in fire-suppressed pine flatwoods wetlands. Fire Ecology 8:96–109

Gorman TA, Powell SD, Jones KC, Haas CA (2014) Microhabitat characteristics of egg deposition sites used by reticulated flatwoods salamanders. Herpetological Conservation and Biology 9:543–550

Hartel T, Nemes S, Cogălniceanu D, Öllerer K, Schweiger O, Moga CI, Demeter L (2007) The effect of fish and aquatic habitat complexity on amphibians. Hydrobiologia 583:173–182

Hayashi M, Rosenberry DO (2002) Effects of ground water exchange on the hydrology and ecology of surface water. Groundwater 40:309–316

Healy RW, Cook PG (2002) Using groundwater levels to estimate recharge. Hydrogeology Journal 10:91–109

Hill EP (2013) *Ambystoma cingulatum* (frosted flatwoods salamander): courtship and oviposition. Herpetological Review 44:113–114

Hill AJ, Durchholz B (2015) Specific yield functions for estimating evapotranspiration from diurnal surface water cycles. Journal of the American Water Resources Association 51:123–132

Hill AJ, Neary VS (2007) Estimating evapotranspiration and seepage for a sinkhole wetland from diurnal surface-water cycles. Journal of the American Water Resources Association 43:1373–1382

Hiscock KM, Bense VF (2014) Hydrogeology: principles and practice, 2nd edn. Wiley-Blackwell, Hoboken

Holbrook JD, Dorn NJ (2016) Fish reduce anuran abundance and decrease herpetofaunal species richness in wetlands. Freshwater Biology 61:100–109

Kirkman LK (1995) Impacts of fire and hydrological regimes on vegetation in depression wetlands of southeastern USA. In: Cerulean SI, Engstrom RT (eds) Fire in wetlands: a management perspective. Proceedings of the Tall Timbers Fire Ecology Conference 19. Tall Timbers Research Station, Tallahassee, pp 10–20

Lu J, Sun G, McNulty SG, Amatya DM (2005) A comparison of six potential evapotranspiration methods for regional use in the southeastern United States. Journal of the American Water Resources Association 41:621–633

Lu J, Sun G, McNulty SG, Comerford NB (2009) Sensitivity of pine flatwoods hydrology to climate change and forest management in Florida, USA. Wetlands 29:826–836

Martin KL, Kirkman LK (2009) Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the southeastern USA. Journal of Applied Ecology 46:906–914

McLaughlin DL, Cohen MJ (2013) Realizing ecosystem services: wetland hydrologic function along a gradient of ecological condition. Ecological Applications 23:1619–1631

McLaughlin DL, Cohen MJ (2014) Ecosystem specific yield for estimating evapotranspiration and groundwater exchange from diel surface water variation. Hydrological Processes 28:1495–1506

Mitsch WJ, Gosselink JG (2007)

Mohamed YA, Bastiaanssen WGM, Savenije HHG, van den Hurk BJJM, Finlayson CM (2012) Wetland versus open water evaporation: an analysis and literature review. Physics and Chemistry of the Earth 47:114–121

Monteith JL (1965) Evaporation and environment. In: Fogg GE (ed) the state of movement of water in living organisms. Society for Experimental Biology (Great Britain), Symposium No. 19. Cambridge University Press, Cambridge, pp 205–234

Morey S, Reznick D (2000) A comparative analysis of plasticity in larval development in three species of spadefoot toads. Ecology 81:1736–1749

Muggeo VM (2015) Regression models with breakpoints/changepoints estimation. R package version 0.5-1.1. http://www.R-project.org

Orellana F, Verma P, Loheide SP, Daly E (2012) Monitoring and modeling water-vegetation interactions in groundwater-dependent ecosystems. Reviews of Geophysics 50:RG3003

Palis JG (1997) Distribution, habitat, and status of the flatwoods salamander (*Ambystoma cingulatum*) in Florida. Herpetological Natural History 5:53–65

Palis JG, Aresco MJ, Kilpatrick S (2006) Breeding biology of a Florida population of Ambystoma cingulatum (Flatwoods Salamander) ?during a drought. Southeastern Naturalist 5:1–8

Park J, Botter G, Jawitz JW, Rao PSC (2014) Stochastic modeling of hydrologic variability of geographically isolated wetlands: effects of hydro-climatic forcing and wetland bathymetry. Advances in Water Resources 69:38–48

Pechmann JHK, Scott DE, Gibbons JW, Semlitsch RD (1989) Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3–11

Porej D, Hetherington TE (2005) Designing wetlands for amphibians: the importance of predatory fish and shallow littoral zones in structuring of amphibian communities. Wetlands Ecology and Management 13:445–455

R Core Team (2014) R: a language and environment for statistical computing. R foundation for statistical computing. Vienna, Austria. http://www.R-project.org

Riekerk H, Korhnak LV (2000) The hydrology of cypress wetlands in Florida pine flatwoods. Wetlands 20:448–460

Russell KR, Guynn DC Jr, Hanlin HG (2002) Importance of small isolated wetlands for herpetofaunal diversity in managed, young growth forests in the Coastal Plain of South Carolina. Forest Ecology and Management 163:43–59

Ryan JA, Ulrich JM (2014) eXtensible time series. R package version 0.9-7. http://www.R-project.org

Sánchez-Carrillo S, Angeler DG, Sánchez-Andrés R, Alvarez-Cobelas M, Garatuza-Payán J (2004) Evapotranspiration in semi-arid wetlands: relationships between inundation and the macrophyte-cover: open-water ratio. Advances in Water Resources 27:643–655

Scott DE (1994) The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology 75:1383–1396

Sekerak CM, Tanner GW, Palis JG (1996) Ecology of flatwoods salamander larvae in breeding ponds in Apalachicola National Forest. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 50:321–330

Semlitsch RD (2002) Critical elements for biologically based recovery plans of aquatic breeding amphibians. Conservation Biology 16:619–629

Semlitsch RD, Wilbur HM (1988) Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. Copeia 1988:978–983

Semlitsch RD, Scott DE, Pechmann JHK, Gibbons JW (1996) Structure and dynamics of an amphibian community: evidence from a 16-yr study of a natural pond. In: Cody ML, Smallwood JD (eds) Long-term studies of vertebrate communities. Academic, New York, pp 217–248

Sharitz RR (2003) Carolina bay wetlands: unique habitats of the southeastern United States. Wetlands 23:550–562

Skelly DK (1997) Tadpole communities: pond permanence and predation are powerful forces shaping the structure of tadpole communities. American Scientist 85:36–45

Snodgrass JW, Komoroski MT, Bryan AL Jr, Burger J (2000) Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. Conservation Biology 14:414–419

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available at: http://websoilsurvey.nrcs.usda.gov/. Accessed April 25th, 2016

Sumner DM (2007) Effects of capillarity and microtopography on wetland specific yield. Wetlands 27:693–701

Sutter RD, Kral R (1994) The ecology, status, and conservation of two non-alluvial wetland communities in the South Atlantic and Eastern Gulf coastal plain, USA. Biological Conservation 68:235–243

Taylor BE, Scott DE, Gibbons JW (2006) Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. Conservation Biology 20:792–801

Thornthwaite CB (1948) Factors affecting evaporation from plants and soils. Journal of Soil and Water Conservation 12:221–227

Tiner RW (2003) Geographically isolated wetlands of the United States. Wetlands 23:494–516

United States Department of the Interior, Fish and Wildlife Service (2009) Endangered and threatened wildlife and plants; Determination of endangered status for reticulated flatwoods salamander; Designation of critical habitat for frosted flatwoods salamander and reticulated flatwoods salamander. Federal Register 74:6700–6774

Werner EE (1986) Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. The American Naturalist 128:319–341

Whiles MR, Goldowitz BS (2001) Hydrologic influences on insect emergence production from central Platte River wetlands. Ecological Applications 11:1829–1842

Wilbur HM, Collins JP (1973) Ecological aspects of amphibian metamorphosis. Science 182:1305–1314

Winter TC, LaBaugh JW (2003) Hydrologic considerations in defining isolated wetlands. Wetlands 23:532–540

Zeileis A, Grothendieck G, Ryan JA, Andrews F (2015) S3 Infrastructure for regular and irregular time series (Z's ordered observations). R package version 1.7-11. http://www.R-project.org