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ORIGINAL RESEARCH

The Effects of Habitat Structure on Winter Aquatic Invertebrate and Amphibian Communities in Pine Flatwoods Wetlands

Houston C. Chandler[1] · **Carola A. Haas**[1] · **Thomas A. Gorman**[1]

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Abstract Natural disturbances play a critical role in structuring many ecosystems. In the southeastern United States, fire suppression and exclusion have removed the natural disturbance regime from many ecosystems, including ephemeral wetlands embedded within longleaf pine forests. We sampled aquatic invertebrate and amphibian communities in 21 pine flatwoods wetlands in northwest Florida from 2012 to 2014. Our objectives were to quantify amphibian and invertebrate community structure, identify differences in amphibian communities across an environmental gradient, and identify how invertebrate communities responded to wetland habitat characteristics. Amphibian communities were more diverse in wetlands with longer hydroperiods but were similar across wetlands with different vegetation structures. To examine the effects of wetland characteristics on aquatic invertebrate communities, we created a set of a priori models relating the abundance of isopods, chironomids, and damselflies to wetland characteristics. The best-approximating models indicated that isopods and damselflies were more abundant in wetlands that were not fire-suppressed. Similarly, total invertebrate abundance was higher in sections of wetlands with low canopy cover when compared to sections of the same wetlands with high canopy cover. Restoration of vegetation structure in wetlands that have experienced long-term fire suppression and wetlands that support longer hydroperiods should be a management priority.

Keywords Amphibians · Aquatic invertebrates · Ephemeral wetlands · Fire · Pine flatwoods

Introduction

Habitat loss, fragmentation, and degradation are considered the primary threats facing many ecosystems (Fahrig 1997; Cushman 2006). Over time, habitat degradation can lead to changes in ecosystem processes and cause shifts in community composition as sensitive species often lack the ability to adapt to rapid changes in environmental characteristics (Casatti et al. 2006; Ernst et al. 2006). Limited dispersal abilities or environmental barriers may also prevent some populations from shifting their distribution away from degraded habitat, which can cause local extirpations (Reinhardt et al. 2005). In lentic freshwater systems, many species lack the ability to actively disperse from one waterbody to another, except during extreme events (e.g. floods) or during certain life stages. Thus, habitat degradation that affects an entire waterbody has the potential to alter aquatic community composition and affect landscape level connectivity by creating waterbodies with inhospitable environmental characteristics for sensitive species (Amezaga et al. 2002).

Small ephemeral wetlands are common landscape features in many ecosystems. A regular drying phase creates unique ecological challenges for aquatic species, and many aquatic organisms inhabiting ephemeral wetlands possess adaptations to persist through regular dry periods including leaving the wetland, retreating below ground, or reaching a desiccation-resistant life-stage (Williams 1985). Species that cannot survive through drying events or that are slow to recolonize newly-filled wetlands are generally excluded from ephemeral wetlands. This includes large predatory fish species, thereby reducing the predation pressure on other members of the

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✉ Houston C. Chandler
houstonc@vt.edu

[1] Department of Fish and Wildlife Conservation, Virginia Tech, 310 West Campus Drive, MC 0321, Blacksburg, VA 24061, USA

aquatic community (Skelly 1997). A reduction in predation pressure combined with the ecological challenges associated with living in a dynamic environment often leads to the development of diverse amphibian (Russell et al. 2002) and aquatic invertebrate communities (Wiggins et al. 1980; Batzer and Wissinger 1996). These communities frequently contain endemic species that depend solely on ephemeral wetlands to provide suitable breeding habitat (Zedler 2003; Gorman et al. 2013).

In temporary wetlands, aquatic invertebrate communities are often complex, reach high densities, and function at multiple trophic levels (Wiggins et al. 1980; Batzer and Wissinger 1996). Similarly, many amphibian species use temporary wetlands as sites for explosive breeding events, and amphibians act as predators and primary consumers in aquatic food webs (Pechmann et al. 1989; Russell et al. 2002). Amphibian larvae also provide a food source for other amphibians, reptiles, predatory invertebrates, birds, and mammals (Wilbur 1997). High population densities and a lack of fish predators can lead to complex community interactions between amphibians and aquatic invertebrates. Many aquatic invertebrates are primary consumers that feed on algae and submerged vegetation, leading to direct competition with anuran larvae (Morin et al. 1988). Some predatory amphibians such as larval salamanders feed primarily on aquatic invertebrates during their larval period (Whiles et al. 2004). However, other aquatic invertebrates such as diving beetles and dragonfly nymphs are apex predators in fishless wetlands (Batzer and Wissinger 1996; Cobbaert et al. 2010). Depending on the vegetation type and litter quality, some invertebrates may also affect decomposition rates and other environmental processes (Kok and Van Der Velde 1994). Given the diversity in ephemeral wetlands and the complex interactions between aquatic invertebrates and amphibians, it is important to understand how these groups respond to habitat change.

The southeastern United States supports a high diversity of ephemeral wetlands (Sutter and Kral 1994; Russell et al. 2002), but this region has experienced severe loss and degradation of wetland resources from anthropogenic disturbance (Hefner and Brown 1984). Pine flatwoods, a type of longleaf pine forest found in low-lying, poorly drained areas of the coastal plain, are characterized by the presence of shallow ephemeral wetlands (Means 1996). These forests are similar to other pine forests of the southeastern U.S. in that they were historically fire-maintained (Frost 1995; Glitzenstein et al. 1995). However, a long history of fire suppression and an inability of dormant-season fires (the typical season for setting prescribed burns) to burn through submerged wetland basins has altered the vegetation structure in many pine flatwoods wetlands (Bishop and Haas 2005). Historically, these wetlands had a relatively open canopy with thick herbaceous vegetation covering wetland basins, but a lack of regular fire creates a dense woody midstory (Kirkman 1995; Hinman and Brewer 2007; Martin and Kirkman 2009). The development of a woody midstory increases canopy cover, decreases the amount of herbaceous vegetation present in wetland basins, alters leaf litter inputs, and decreases the amount of solar radiation reaching the wetland basin (Hinman and Brewer 2007). The effects of changing vegetation structure on the composition of faunal aquatic communities in pine wetlands have not been well studied (Jones et al. 2010).

The goals of our study were to characterize the habitat and aquatic communities in pine flatwoods wetlands that have experienced varying degrees of habitat succession and are part of ongoing adaptive management projects (Gorman et al. 2013). First, we describe the vegetation structure of the study wetlands and quantify the amphibian and invertebrate communities in these wetlands. Second, we use the substantial variation in wetland vegetation characteristics and wetland hydroperiod to examine how variation in habitat characteristics affects amphibian community composition. Finally, we examine the relative influence of different habitat characteristics on invertebrate abundance both among and within wetlands.

Methods

Study Sites

We sampled 21 ephemeral wetlands located on Eglin Air Force Base in Okaloosa County, Florida from 2012–2014. Eglin AFB is a large military installation containing over 146,000 ha of actively managed longleaf pine forests. We focused our sampling efforts from December to April as this is the typical period when these wetlands hold water. We sampled 21 wetlands that were part of ongoing adaptive management projects designed to lower canopy cover and increase herbaceous vegetation cover by removing the woody midstory present in many wetlands. All mechanical treatments were applied prior to the beginning of the 2012 sampling season (see Gorman et al. 2013 for a complete description of the management prescriptions). Before the 2012 sampling season, we established a transect in each of the 21 wetlands that began in the ecotone and ran along the wetland's longest axis. We marked sampling points along this transect every 20 m in small wetlands and every 40 m in five wetlands larger than 1.5 ha. Established points in the wetland basins were used to perform the sampling conducted during this study.

Amphibian Sampling

We sampled amphibians in the 21 wetlands using multiple techniques during both years. All sampling was dependent on the presence of water in each wetland, so the number of sampling events varied among wetlands and between years.

From December to April, we conducted nighttime call surveys twice a month at each wetland that had water. Each survey consisted of a 5-min listening period where we recorded all calling anurans (Gorman et al. 2013). On each occasion, we conducted one call survey at each end of a wetland (two surveys per wetland). We also performed dipnetting surveys targeting reticulated flatwoods salamander (*Ambystoma bishopi*) larvae, which is a federally endangered species that relies primarily on pine flatwoods wetlands for breeding habitat. We used a 3-mm mesh SH-2 or SH-2D dipnet (Mid-Lakes Corporation, Knoxville, Tennessee) to sample areas with dense herbaceous vegetation (Gorman et al. 2009a). Surveys were performed for 30 min in each wetland, once or twice a month from December to April, depending on water levels. Even though flatwoods salamander larvae were the focus of these surveys, the habitat sampled is used by multiple species of amphibians, and all captured amphibians were identified to species.

Aquatic Invertebrate Sampling

We sampled aquatic invertebrates along the pre-established transect in each wetland once a month from January to April 2014. We used a 1-mm mesh dipnet (SH-2D, Mid-Lakes Corporation, Knoxville, Tennessee) to sample aquatic invertebrates along the entire wetted length of the transect (this length changed from month to month depending on the water level). We performed five approximately 1 m dipnet sweeps every 20 m. Dipnets were swept through the water column just above the bottom and through any herbaceous vegetation. Dipnet sweeps were approximately evenly spaced along the 20 m between each point. We identified and counted all aquatic invertebrates to the lowest taxonomic level possible in the field prior to releasing them.

Habitat Surveys

We sampled multiple habitat characteristics along the pre-existing transect in each wetland. We used a point-centered quarter method (Cottam and Curtis 1956), where we measured the distance to the nearest tree (DBH >7.6 cm) and shrub (DBH <7.6 cm) in each of the four cardinal directions. We identified all trees and shrubs to species. The total distance to the nearest shrub was used to estimate a shrub density for the entire wetland (Mitchell 2007). We used a Daubenmire (1959) frame (0.5×0.2 m rectangular plot) and cover class scale to estimate the total cover class of all herbaceous vegetation species. The total cover class for each sampling point was averaged to generate an estimate of percent herbaceous vegetation cover for an entire wetland. We used a convex spherical densiometer to measure canopy cover in each wetland. Canopy cover measurements were recorded in each of the four cardinal directions at each sampling point and halfway in between each pair of points. We averaged all canopy cover measurements to create a single canopy cover estimate for each wetland. Canopy cover measurements were recorded during spring 2014, and all other vegetation measurements were recorded during fall 2013.

Additionally, we sampled water depth in each wetland. Depth measurements were recorded at an approximate center point in each wetland (located along the pre-existing transect). Depth measurements were recorded twice a month from October to April and once a month the rest of the year. We calculated the average depth in each wetland from January to April 2014 because this was the time period when all invertebrate sampling was conducted. Then we calculated an average hydroperiod from 2010 to 2014 (a longer period should generate a more accurate representation of the hydroperiod through time) for each wetland using the same depth measurements from the approximate center point. We identified the longest yearly (September-August) hydroperiod that occurred at least partially between October and April and used these yearly hydroperiods to calculate an average for each wetland.

Statistical Analyses

To examine the effects of habitat on amphibian communities, we categorized each wetland using two criteria: 1) herbaceous vegetation and canopy cover and 2) the average hydroperiod. First, we categorized all wetlands as having either high vegetation quality (>30 % herbaceous vegetation cover and <50 % canopy cover) or low vegetation quality (<20 % herbaceous vegetation cover and >50 % canopy cover). Wetlands that did not fit into either category (e.g. low canopy cover and low herbaceous vegetation cover) were grouped into a third category (medium vegetation quality). Second, we categorized all wetlands as having a long hydroperiod (5–7 months), a mid-length hydroperiod (3–5 months), or a short hydroperiod (<3 months). All 21 wetlands were included in the vegetation and hydroperiod categories, and we only compared within, not between, the vegetation and hydroperiod categories. To examine amphibian community composition, we visualized the community data using non-metric multidimensional scaling (NMDS) plots. We created NMDS plots using Bray-Curtis dissimilarities. We then assessed the amphibian community composition among different wetland categories using distance-based permutational multi-variate analysis of variance (PERMANOVA). We performed PERMANOVA on each grouping of wetlands using Bray-Curtis dissimilarity indices to calculate distances using 999 permutations. Lastly, we performed pairwise PERMANOVA comparisons for all categories if there was a significant difference for the omnibus test. NMDS and PERMANOVA were conducted using the R package vegan (Oksanen et al. 2015).

Invertebrate abundance was calculated as the number of invertebrate captures per wetland standardized by the number of dipnet sweeps conducted in that wetland. We used multiple linear regression models to examine the effects of habitat on the three most abundant invertebrate groups (isopods, damselflies, and chironomid midges). Our predictor variable set included percent canopy cover, percent herbaceous vegetation cover, shrub density, average water depth, and average hydroperiod, which are all biologically relevant factors for invertebrate communities (Carpenter and Lodge 1986; Batzer and Resh 1991; Batzer and Wissinger 1996; Zimmer et al. 2000). We developed a priori hypotheses by using these five variables to test the importance of vegetation structure (percent canopy cover, percent herbaceous vegetation cover, shrub density), hydrology (average water depth and average hydroperiod), and both vegetation structure and hydrology combined. Using our five predictor variables, finding no problems with multicollinearity, we created 31 models for each of the three invertebrate groups.

We used an information theoretic approach and Akaike's Information Criterion corrected for small sample sizes (AICc) to evaluate the strength of a priori hypotheses (Burnham and Anderson 2002). We considered the model with the lowest AICc to have the best balance of statistical parsimony and goodness of fit for the data. We also calculated AICc weights (*w*), which range from 0 to 1, with the best fitting model having the highest weight. We considered models with a ΔAICc value of <2 to be well supported by the data and models with a ΔAICc value >2 and <4 to be moderately supported (Burnham and Anderson 2002). We used the best-approximating model for each invertebrate group to evaluate habitat preferences among these groups. We also calculated the relative importance of each predictor variable in a model set by summing the AICc weights for all models containing that variable (Burnham and Anderson 2002). All AIC values were calculated using the R package AICcmodavg (Mazerolle 2014).

To further examine the effects of habitat on invertebrate communities, we identified six wetlands with sections of high and low canopy cover within the same wetland. In this case, low canopy cover sections were defined as having an average canopy cover of <40 %, and high canopy cover sections were defined as having an average canopy cover of >65 %. We used two-sample t-tests to compare the total invertebrate abundance in high and low canopy sections of these six wetlands on a monthly basis. All analyses were performed in R (R Core Team 2014).

Results

Habitat Characteristics

We observed substantial variation in vegetation characteristics among the 21 wetlands, ranging from open canopies and almost continuous herbaceous vegetation cover to dense shrubs, thick canopies, and almost no herbaceous vegetation (Table 1). There were also some wetlands with open canopies but little herbaceous vegetation because of recent restoration and management activities. Slash pine (*Pinus elliottii*) and longleaf pine (*Pinus palustris*) were the most abundant tree species in the study wetlands. Shrub diversity was high throughout the study sites. There was also a high diversity of herbaceous vegetation encountered, but wiregrass (*Aristida stricta*) was the most abundant species (see Chandler 2015 for a more detailed description of wetland plant communities). However, there were also nine wetlands where thick leaf litter and bare ground dominated the majority of the sampling points (i.e. no herbaceous vegetation). In addition to the variation in wetland vegetation communities, wetland depths and hydroperiods were variable among wetlands and through time (e.g. 2013 characterized by drought and 2014 characterized by well-above average precipitation; Table 1).

Amphibian Communities

From 2012 to 2014, we identified 17 amphibian species (14 anurans and 3 caudates) in the 21 study wetlands (Table 2). The number of species per wetland ranged from 2 to 11 with an average of six species per wetland. Southern cricket frogs (*Acris gryllus*) and southern leopard frogs (*Lithobates spenocephalus*) were the amphibian species most commonly encountered during amphibian surveys (100 and 95 % of sites occupied, respectively). Pine woods treefrogs (*Hyla femoralis*) were also commonly encountered on call surveys, but larvae were never captured during dipnetting surveys (81 % of sites occupied). *Lithobates sphenocephalus* was the most abundant species (474 of 857 amphibian dipnetting captures). Together, *A. gryllus*, *L. sphenocephalus*, and ornate chorus frogs (*Pseudacris ornata*) accounted for 86 % of amphibian dipnetting captures from 2012 to 2014. We also

Table 1 Mean habitat characteristics for 21 pine flatwoods wetlands located on Eglin Air Force Base, Florida. Hydroperiod measurements represent an average of the longest yearly hydroperiod occurring partially between October and April from 2010 to 2014. Vegetation measurements were recorded once in each wetland during fall 2013 or, for canopy cover, spring 2014. Depth measurements represent the average depth (measured bimonthly) at an approximate center point from January to April 2014

	Mean	SE	Min	Max
Canopy cover (%)	48.33	4.03	18.00	81.80
Herbaceous cover (%)	25.28	4.77	2.50	84.38
Shrub density (per m)	0.99	0.14	0.40	2.67
Average depth (cm)	29.07	2.98	4.60	63.60
Hydroperiod (months)	4.29	0.29	2.30	6.60

Table 2 Amphibian species recorded in 21 pine flatwoods wetlands on Eglin Air Force Base, Florida from 2012 to 2014. Wetlands were categorized as having high-quality vegetation (herbaceous vegetation cover >30 % and canopy cover <50 %), low-quality vegetation (herbaceous vegetation cover <20 % and canopy cover >50 %), or medium-quality vegetation (wetlands that did not meet both criteria for either group). Wetlands were also categorized by the length of their average hydroperiod from 2010 to 2014 (long: 5–7 months, medium: 3–5 months, and short: <3 months). The number of wetlands in each category is indicated in parentheses

	Vegetation Quality			Hydroperiod		
Species	High (8)	Med (5)	Low (8)	Long (7)	Med (10)	Short (4)
Southern Cricket Frog (*Acris gryllus*)	8	5	8	7	10	4
Southern Leopard Frog (*Lithobates sphenocephalus*)	7	5	8	7	9	4
Ornate Chorus Frog (*Pseudacris ornata*)	6	5	3	6	7	1
Pine Woods Treefrog (*Hyla femoralis*)	5	4	8	6	8	3
Southern Chorus Frog (*Pseudacris nigrita*)	4	2	2	3	4	1
Oak Toad (*Anaxyrus quercicus*)	2	3	3	5	3	0
Reticulated Flatwoods Salamander (*Ambystoma bishopi*)	2	3	1	2	4	0
Southern Toad (*Anaxyrus terrestris*)	2	2	2	2	4	0
Pig Frog (*Lithobates grylio*)	2	2	2	5	1	0
Eastern Newt (*Notophthalmus viridescens*)	2	2	2	3	3	0
Dwarf Salamander (*Eurycea quadridigitata*)	1	3	1	1	3	1
Barking Treefrog (*Hyla gratiosa*)	1	1	1	3	0	0
Eastern Narrow-mouthed Toad (*Gastrophryne carolinensis*)	1	1	0	1	1	0
Green Frog (*Lithobates clamitans*)	0	1	5	3	3	0
Green Treefrog (*Hyla cinerea*)	0	1	0	1	0	0
Squirrel Treefrog (*Hyla squirella*)	0	1	0	1	0	0
Bog Frog (*Lithobates okaloosae*)	0	1	0	1	0	0

identified a single Florida bog frog (*Lithobates okaloosae*), a species endemic to northwestern Florida, calling from one study wetland, which is notable as this species usually breeds in steephead ravines (Enge 2005) and slow moving sections of streams (but one individual was previously detected calling from an isolated cypress dome; Gorman et al. 2009b).

There were no differences between amphibian communities across a range of wetland vegetation structures despite substantial variation in canopy and herbaceous vegetation cover (*pseudo-F*=1.78, *P*=0.09; Fig. 1a). Amphibian communities were dissimilar across a range of wetland hydroperiods (*pseudo-F*=2.16, *P*=0.03; Fig. 1b). Wetlands with long hydroperiods were dissimilar from wetlands with short hydroperiods (*pseudo-F*=4.57, *P*=0.006) but not wetlands with medium hydroperiods (*pseudo-F*=1.09, *P*=0.40). Wetlands with short hydroperiods were also not different from wetlands with medium hydroperiods (*pseudo-F*=2.00, *P*=0.14). Furthermore, long hydroperiod wetlands had more diverse amphibian communities (8.1±0.8 species) than short hydroperiod wetlands (3.5±0.5 species; t_9=4.07, *P*=0.001).

Invertebrate Communities

From January to April 2014, we captured a total of 30,073 invertebrates during dipnet surveys (Table 3). Isopods (Order Isopoda) accounted for 70.8 % of the total invertebrate captures over the 4-month sampling period. Isopod abundance per wetland ranged from 0.01 to 33.4 captures per dipnet sweep. Non-biting midges (Family Chironomidae) were the second most common invertebrate captured (6.2 %) followed closely by damselfly nymphs (Suborder Zygoptera) at 5.6 %. Chironomid midge abundance ranged from 0.1 to 4.6 captures per dipnet sweep, and damselfly abundance ranged from 0.0 to 2.2 captures per dipnet sweep. Other groups were locally abundant in some wetlands but were uncommon at a landscape scale. For example, phantom midges (Family Chaoboridae) accounted for 71 % (605 individuals) of the total captures in one wetland, but only 46 individuals were captured in the remaining 20 wetlands. Other groups were commonly encountered in a majority of wetlands including backswimmers (Family Notonectidae), boatmen (Family Corixidae), and mosquito larvae (Family Culicidae). Large predatory invertebrates (e.g. Belostomatidae and Cambaridae) were rarely encountered during dipnet surveys but were often seen at night during spotlighting surveys (Chandler unpublished data).

Our modeling results indicated that a mix of vegetation and hydrologic characteristics influenced invertebrate abundance in pine flatwoods wetlands. For isopods, the best-approximating model included variables for canopy cover and shrub density (Table 4), and both canopy cover and shrub density had a negative effect on isopod abundance (Table 5).

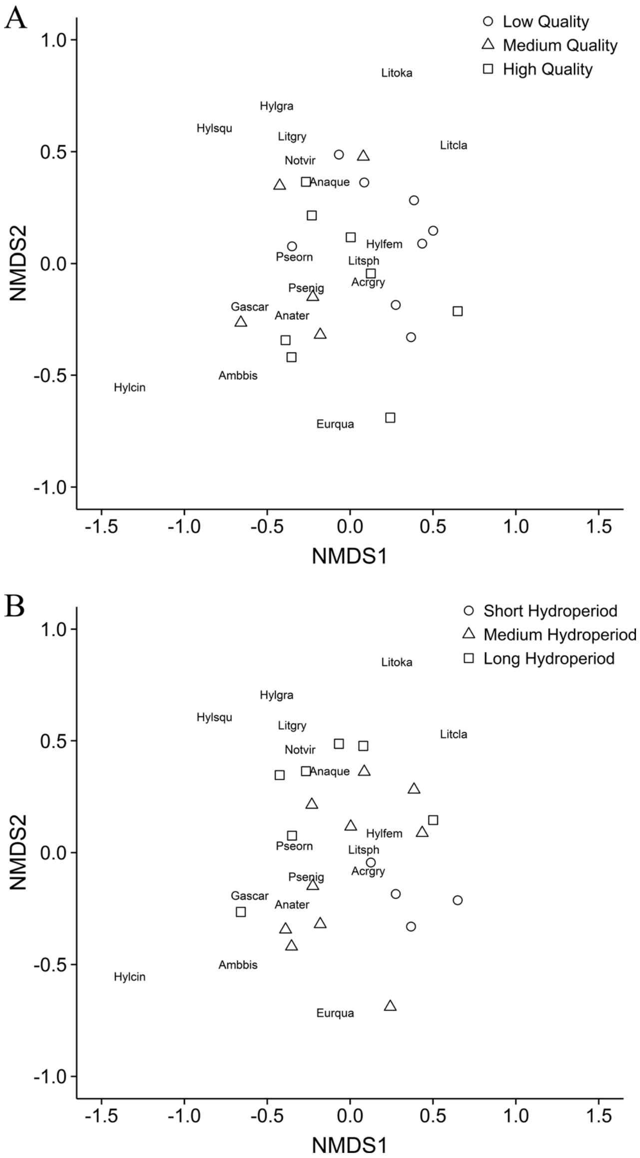


Fig. 1 Ordination plot of the first and second axes from non-metric multidimensional scaling (NMDS) on amphibian communities found in 21 pine flatwoods wetlands on Eglin Air Force Base, Florida. Wetlands were divided using two criteria: **a** vegetation quality and **b** wetland hydroperiod. All 21 wetlands were included in both categories. *Shapes* represent different wetlands, and *letters* represent species codes (first three letters of genus + first three letters of species name). NMDS plots were plotted using Bray-Curtis dissimilarities

No other models had a ΔAICc value <2, while six models had a ΔAICc between 2 and 4. These six moderately-supported models mostly contained variables relating to vegetation characteristics. Canopy cover and shrub density also had the highest relative importance among the predictor variables (Canopy Cover=0.79; Shrub Density=0.75; Herbaceous Cover=0.37; Hydroperiod=0.19; Depth=0.17).

There were two models with ΔAICc values <2 in the damselfly (Zygoptera) model set (Table 4). The best-approximating model included variables for canopy cover and hydroperiod. The other well-supported model contained variables for canopy cover, shrub density, and hydroperiod. Canopy cover and shrub density had a negative effect on damselfly abundance, but damselfly abundance was positively related to hydroperiod (Table 5). Three models received moderate support. All three moderately-supported models included the canopy cover variable and either the hydroperiod or depth variable. Canopy cover and hydroperiod had high relative importance among the predictor variables, while shrub density had a low relative importance (Canopy Cover=0.97; Hydroperiod=0.81; Shrub Density=0.33; Depth=0.23; Herbaceous Cover=0.19).

The best-approximating model for chironomid midge abundance included variables for depth and hydroperiod (Table 4). Depth had a positive effect on chironomid midge abundance, while the effect of hydroperiod was not significant (Table 5). Three other models had a ΔAICc <2, and 13 models were moderately supported. The remaining well-supported models included only a single factor in each model (depth, herbaceous cover, and canopy cover, respectively; Table 4). Moderately-supported models contained all five potential variables. Depth and hydroperiod had the highest relative importance among predictor variables, but the relative importance of all five variables was similar (Depth=0.59; Hydroperiod=0.44; Canopy Cover=0.33; Herbaceous Cover=0.32; Shrub Density=0.22).

Finally, invertebrate abundance was significantly higher in low canopy cover sections of six wetlands when compared to high canopy cover sections of the same wetlands from February to April (January: $t_5=1.78$, $P=0.07$; February: $t_5=2.60$, $P=0.02$; March: $t_5=2.76$, $P=0.02$; April: $t_5=2.83$, $P=0.02$; Fig. 2). The average canopy cover in high canopy sections was 73 % compared to just 31 % in the low canopy sections. Average invertebrate abundance in high canopy cover sections was 5.1 (SE=0.79) captures per dipnet sweep compared to 17.3 (SE=3.46) captures per sweep in low canopy cover sections.

Discussion

We documented that, as a whole, amphibian communities were more likely to respond to differences in wetland hydroperiod than to differences in wetland vegetation characteristics. Amphibian communities in wetlands with long hydroperiods were more diverse than in wetlands with short hydroperiods, and many amphibian species are more likely to successfully reproduce in wetlands with a longer hydroperiod as long as the wetland remains ephemeral (Snodgrass et al. 2000; Amburgey et al. 2014). Amphibians present in wetlands with long hydroperiods that were absent in wetlands with shorter hydroperiods tended to be species with long development times (e.g. *A. bishopi*) or species that breed later in the

Table 3 Total invertebrate captures from dipnetting surveys conducted once a month from January to April 2014 in 21 pine flatwoods wetlands on Eglin Air Force Base, Florida. Surveys were conducted using a 1-mm mesh dipnet, and invertebrates were identified to the lowest possible taxonomic level in the field

Phylum (Subphylum)	Class	Order (Suborder)	Family	Species	Total	% Captures
Annelida	Oligochaeta				57	0.19
Arthropoda (Chelicerata)	Arachnida	Trombidiformes			52	0.17
Arthropoda (Crustacea)	Malacostraca	Isopoda			21,281	70.76
		Amphipoda			441	1.47
		Decapoda	Cambaridae	*Procambarus sp.*	27	0.09
				P. evermanni	12	0.04
				P. hubbelli	1	0.003
	Branchiopoda	Anostraca			983	3.27
Arthropoda (Uniramia)	Insecta	Hemiptera (Heteroptera)	Corixidae		501	1.67
			Notonectidae		1165	3.87
			Belostomatidae		6	0.02
			Gerridae		131	0.44
		Coleoptera			432	1.44
			Gyrinidae		33	0.11
			Dytiscidae		32	0.11
			Hydrophilidae		3	0.01
		Odonata (Zygoptera)			1683	5.60
		Odonata (Anisoptera)			61	0.20
			Aeshnidae		35	0.12
			Libellulidae		139	0.46
		Ephemeroptera			15	0.05
		Diptera			9	0.03
			Culicidae		399	1.33
			Chaoboridae		651	2.16
			Chironomidae		1871	6.22
			Tabanidae		1	0.003
			Ceratopogonidae		52	0.17

year when many short hydroperiod wetlands may have already dried (e.g. members of the genera *Hyla* and *Lithobates*).

In contrast to the observed differences in amphibian communities across a hydroperiod gradient, amphibian communities were similar over a range of canopy and herbaceous vegetation cover. Many of the species identified in our surveys are habitat generalists that likely do not respond to vegetation structure (e.g. *Acris gryllus* and *Lithobates*

Table 4 Multiple linear regression modeling results relating invertebrate abundance to vegetation characteristics and wetland hydrology in pine flatwoods wetlands on Eglin Air Force Base, Florida (AICc= second-order Akaike's Information Criteria, K=the number of parameters, ΔAICc= change in AICc, and w_i=relative amount of support for each model)

Candidate Models	AICc	K	ΔAICc	w_i
Isopoda				
Canopy Cover+Shrub Density	145.9	4	0	0.32
Zygoptera				
Canopy Cover+Hydroperiod	35.6	4	0	0.34
Canopy Cover+Shrub Density+Hydroperiod	36.5	5	0.96	0.21
Chironomidae				
Depth+Hydroperiod	61.0	4	0	0.15
Depth	61.6	3	0.58	0.11
Herbaceous Cover	61.8	3	0.80	0.10
Canopy Cover	61.8	3	0.86	0.10

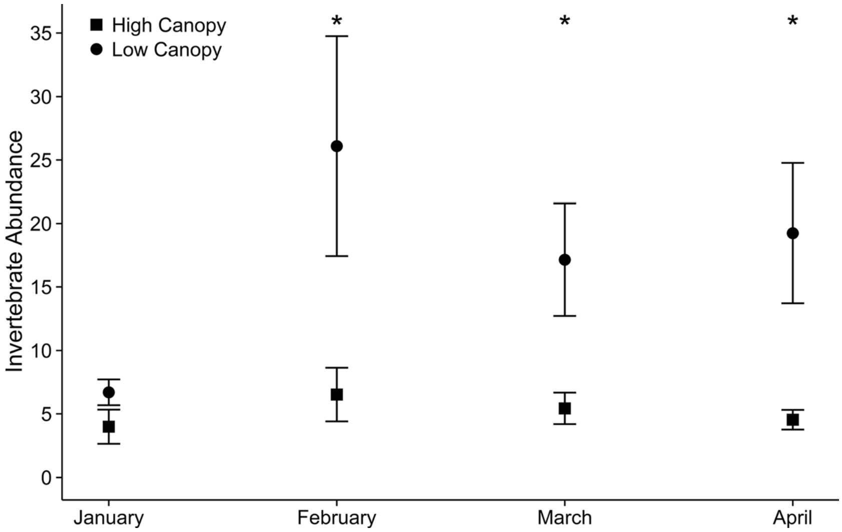
Table 5 Parameter estimates and 95 % confidence intervals for the best-approximating model relating habitat variables to the abundance of three aquatic invertebrate groups in pine flatwoods wetlands. Aquatic invertebrates were sampled once a month from January to April 2014 in 21 ephemeral wetlands on Eglin Air Force Base, Florida

Taxa	Parameter	Estimate	Standard Error	Lower CL	Upper CL
Isopoda	Intercept	30.38	5.21	19.42	41.31
	Canopy Cover	−0.31	0.08	−0.49	−0.14
	Shrub Density	−0.0006	0.0002	−0.001	−0.00008
Zygoptera	Intercept	0.71	0.43	−0.19	1.62
	Canopy Cover	−0.02	0.006	−0.03	−0.009
	Hydroperiod	0.22	0.08	0.05	0.39
Chironomidae	Intercept	0.92	0.66	−0.47	2.30
	Depth	0.05	0.02	0.009	0.08
	Hydroperiod	−0.34	0.18	−0.72	0.05

sphenocephalus). Even though we did not find evidence of a vegetation effect on the overall amphibian community, previous research has indicated that both *A. bishopi* and *P. ornata* are habitat specialists that select breeding sites with open canopies and dense herbaceous vegetation (Gorman et al. 2013). *Pseudacris ornata* likely benefit from the presence of herbaceous vegetation during the larval period (Alford 1986), and *A. bishopi* may benefit from herbaceous vegetation during all life stages (Gorman et al. 2009a, 2014; Jones et al. 2012). The similarity of amphibian communities between wetlands with different vegetation characteristics may also be attributed to fine scale spatial variation (multiple habitat types) within wetlands. Even in fire-suppressed wetlands, occasional ringing fire creates small habitat patches where sensitive species may be able to persist even though a majority of the wetland is characterized by unsuitable habitat.

Invertebrate abundance was lower in pine flatwoods wetlands with high canopy cover, high shrub density, and low herbaceous vegetation cover, characteristics of fire-suppressed wetlands (Bishop 2005; Hinman and Brewer 2007). This relationship was apparent at both broad and fine spatial scales. At a broad spatial scale, our results indicated that aquatic invertebrate abundance responded to both vegetation and hydrology characteristics depending on the invertebrate group. Isopod abundance was strongly influenced by vegetation characteristics. The negative relationship in the best-approximating model between canopy cover and shrub density and isopod abundance suggests that this group prefers pine flatwoods wetlands with a vegetation structure that is consistent with a fire-maintained landscape. Similarly, damselfly nymph abundance was lower when canopy cover was high but was higher in wetlands with a longer hydroperiod, possibly due to a late breeding period and a long development period. Chironomid midge abundance was primarily associated with wetland hydrology rather than vegetation characteristics, but the results were highly variable. This variation may be caused by high diversity in the family Chironomidae (Stagliano et al. 1998; Voshell 2002), which could result in multiple species with different habitat preferences being lumped into one group. Furthermore, many midges in this family may not be large enough to be consistently collected using a 1-mm mesh dipnet, and this likely affected our abundance estimates. At finer spatial scales, canopy cover again appeared to be an important factor influencing invertebrate

Fig. 2 Aquatic invertebrate abundance measured from January to April 2014 in high canopy cover and low canopy cover sections of six pine flatwoods wetlands on Eglin Air Force Base, Florida. *Error bars* represent standard error, and *asterisks* represent months where there was significantly higher invertebrate abundance in low canopy sections



abundance. Overall, these results demonstrate a strong effect of vegetation structure on certain aquatic invertebrate groups similar to those identified for sensitive amphibian species (Gorman et al. 2009a, 2013).

There are multiple pathways through which different vegetation structures could affect aquatic communities. High canopy cover in isolated wetlands can cause decreases in water temperatures, decreases in periphyton growth rates, and decreases in dissolved oxygen (DO) levels (Skelly et al. 2002). Increasing canopy cover and shrub density are also likely to shift litter inputs away from grass-dominated to woody plant based litter (this was evident in many of the study wetlands). Overall, little is known about how leaf litter inputs affect invertebrate communities in ephemeral wetlands and some studies have documented differential effects (Magnusson and Williams 2006; Batzer and Palik 2007). For amphibian larvae, Williams et al. (2008) found that shifting from grass-dominated litter to hardwood tree litter negatively impacted amphibian success, likely because of decreased phytoplankton growth rates. Further, large amounts of organic matter can decrease DO levels during decomposition (Magnusson and Williams 2006). Overgrown ephemeral wetlands often have lower DO levels than restored wetlands with more open canopies, and higher DO levels (greater than 4 mg/L) were shown to increase recruitment in spotted salamanders (*Ambystoma maculatum*; Sacerdote and King 2009). Finally, increasing canopy cover tends to decrease the amount of herbaceous cover in pine wetlands (this relationship was likely weaker in our study sites because of ongoing adaptive management studies; Gorman et al. 2013). The amount of herbaceous cover is often positively associated with invertebrate abundance (Zimmer et al. 2000). Herbaceous vegetation can increase surface area for periphyton growth (Cattaneo and Kalff 1979), enhance litter quality (Williams et al. 2008), increase DO levels (Ma et al. 2013), and provide refugia from predators (Batzer and Resh 1991; Kopp et al. 2006).

Despite the apparent negative impacts of vegetation characteristics on wetlands that experienced long-term fire suppression and exclusion, we documented a diverse assemblage of invertebrates. Invertebrate communities are poorly studied in this habitat type, but we documented similar communities to those previously reported from other pine wetlands (Golladay et al. 1997; Dietz-Brantley et al. 2002). Isopods were the most abundant invertebrate group in our samples, which was unexpected given that this group is susceptible to local extinctions during drying events and does not possess many of the adaptations necessary to persist through drying events (Styron 1968). Isopods may be able to rapidly colonize ephemeral wetlands by moving across the landscape in overwash from other water bodies during precipitation events (this likely represents an important movement vector for many species in this system) or by retreating into crayfish burrows during dry periods (Wiggins et al. 1980). The prevalence of isopods in our samples could have important ecological applications because this group is one of the primary food sources of larval *A. bishopi* (Whiles et al. 2004). It is important to note that our sampling procedures prevented us from identifying invertebrates to genus or species in most cases, and the mesh size on our dipnets prevented us from collecting micro-crustaceans (e.g. copepods and cladocerans), which can also serve as important food sources for larval *A. bishopi* (Whiles et al. 2004). The lack of information about aquatic invertebrate communities in pine flatwoods wetlands suggests that further study is needed.

Over time, habitat degradation can lead to changes in community structure, which can negatively impact ecosystem function (Casatti et al. 2006; Ernst et al. 2006). Our results demonstrate that aquatic invertebrate communities in pine flatwoods wetlands generally respond negatively to habitat conditions that may result from long-term fire suppression and exclusion (Hinman and Brewer 2007). Future research should examine how these changes in invertebrate abundance affect ecosystem function and other members of the aquatic community. Certain amphibian species also respond negatively to vegetation changes associated with fire exclusion (Gorman et al. 2013), and both amphibians and invertebrates can increase landscape level connectivity by linking aquatic and terrestrial environments (Stagliano et al. 1998; Nakano and Murakami 2001; Whiles et al. 2006). In some cases emergent aquatic insect inputs into terrestrial systems may exceed secondary terrestrial production (Bartrons et al. 2013). Therefore, to promote high-quality aquatic habitat, managers should focus on ensuring that wetland basins are effectively burned rather than leaving entire wetlands as unburned pockets during burns of larger areas (Bishop and Haas 2005). Severe drought years may provide a unique opportunity to successfully burn wetlands during a time of year when wetlands would not normally burn. Others have demonstrated that combining regular burns with mechanical and herbicide treatments aimed at reducing woody vegetation in overgrown wetlands could increase the amount of suitable wetland habitat at a landscape scale (Martin and Kirkman 2009; Gorman et al. 2013). Wetlands with longer hydroperiods should be a management priority as these wetlands tend to support higher amphibian diversity (Snodgrass et al. 2000) and provide important breeding habitat for species with long development times (Chandler 2015).

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