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Taxa specific responses to flooding shape patterns of abundance in a river rock pool metacommunity

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Taxa specific responses to flooding shape patterns of abundance in a river rock pool metacommunity

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Environmental Studies at Virginia Commonwealth University

By

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Table of Contents

List of Figures

Abstract

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Connectivity and habitat area are important landscape characteristics that drive patterns of abundance and diversity across scales. However, responses to connectivity and patch size are dependent on species traits. Riverine landscapes are highly dynamic both spatially and temporally with hydrologic connectivity being a major driver of abundance and diversity. Here we modeled densities of the Virginia river snail and skimmer dragonfly nymphys, two taxa with differences in their dispersal abilities and life histories, as a function of flooding, patch area, and season in over 300 riverine rock pools. We found key differences in how each taxon responded to these predictors with increasing pool flood height having a strong negative effect on snail densities and dragonfly nymph densities increasing as pools became more isolated from the river channel. Our study highlights how differences in response to landscape characteristics are dependent on organism traits. These findings give insight into patterns of abundance and diversity across scales.

Introduction

Connectivity and patch size are critical components of landscape structure (Godron 1981;

Taylor et al. 1993). Because of the roles connectivity and patch size play in ecological processes

they underpin prominent theories explaining species abundance and richness across scales

(Simberloff and Wilson 1969; Hanski 1999; Leibold et al. 2004). The degree to which habitats

are connected determines dispersal, colonization rates, species persistence, gene flow, and the

movement of resources within a landscape (Thompson et al. 2017; Frisch et al. 2012; Fahrig and

Merriam 1985; Keyghobadi et al. 2005; Tockner et al. 1999). Similarly, patch size has been

shown to influence population densities and species richness (Bender et al. 1998; Connor et al.

2000; Matter 2000). Often these two processes are considered in conjunction (Hill et al. 1996;

Schuler et al. 2017). Because of global declines in biodiversity associated with habitat

fragmentation, there is considerable interest in how these processes influence population

dynamics and shape patterns of diversity in terrestrial and aquatic habitats (Fuller et al. 2015;

Haddad et al. 2015).

Differences in dispersal modes and abilities as well as life histories of organisms could

lead to asymmetric responses to landscape characteristics. For instance, highly vagile organisms

may not be as sensitive to habitat connectivity as less mobile organisms. (With and Crist 1995;

D'Eon et al. 2002). Likewise, there are observed disparities in responses to patch size that are

associated with species traits (Steffan-Dewenter and Tscharntke 2000; Prugh et al. 2008). These

responses to landscape connectivity and patch size could shape spatial and temporal patterns of

abundance and diversity at the local and landscape scales. In dynamic ecosystems such as

riverine landscapes organisms with different traits and life histories can exploit changes in landscape characteristics that fluctuate over space and time (Robinson et al. 2002).

Aquatic ecologists have recognized the utility of looking at riverine systems through the lens of landscape ecology (Wiens 2002). Linkages between habitat patches may be of even greater importance in riverine systems because of the structural connectivity of free-flowing water. Additionally, hydrological connectivity of habitat patches within riverine landscapes is highly dynamic (Amoros and Bornette 2002). Ward et al. (1989) described connectivity in aquatic habitats in four dimensions: vertical, lateral, longitudinal, and temporal (Ward 1989). In the case of lateral connectivity rivers and their floodplains are coupled by pulses in river discharge (Tockner et al. 2000). In this paper, we focus on the lateral and temporal dimensions of lotic landscape connectivity.

Here we explore how hydrologic connectivity, patch size, and season influence densities of two taxa with different life histories and dispersal abilities in a system of riverine rock pools. Pools are well suited for answering this question because they are numerous in the landscape vary in size, and easily are sampled. Moreover, rock pools are an ideal study system because their spatial and temporal connectivity can be quantified. Pools vary in their distance from and height above the river channel creating a gradient of lateral hydrological connectivity depending on the river stage. We created a flood model for each pool in our study system allowing us to estimate a pool's hydrologic connectivity.

We used data collected over five years to model the densities of skimmer dragonfly nymphs (*Libellulidae, Pantalla* spp*.)* and Virginia river snails (*Pleuroceridae, Elimia virginica*). Each taxon was chosen because of their ability to disperse to rock pools lies on either end of the hydrologic connectivity spectrum. When lateral connectivity is high snails will be able to

colonize and move between rock pools. Conversely, when hydrologic connectivity is low pools will become isolated from the river and snail movement will be restricted. We expect to see the opposite pattern in skimmer dragonflies that colonize pools via oviposition. When pools are inundated dragonflies will be excluded from ovipositing in pools and only when pools become isolated will they be able to colonize them. *Libellulidae* spp., a highly vagile organism, may be able to access all patches within the landscape however, the number of available pools is dependent on river height. Additionally, the longer a pool is isolated from the river the potential for dragonflies to colonize it increases.

Following colonization, we expect that response to flooding will be asymmetric. *Elimia virginica* is adapted to flowing streams and therefore is less likely to be subject to in situ mortality rates and removal by pool flooding to the same degree that *Pantala* spp., which oviposit in lentic freshwater habitats, will be. Therefore, we expect densities of dragonfly nymphs to increase with pool temporal isolation due to higher probabilities of colonization and reductions in mortality associated with decreased flooding. We expect lower snail densities in pools that have been isolated from the river longer because of the potential for higher temperatures and lower dissolved oxygen than pools that have been flooded more recently. For both taxa we expect increased resources associated with larger pool size to sustain higher densities following colonization.

The life history of each taxon is expected to influence their densities in rock pools. Virginia river snails are estimated to have lifespans of several years, therefore they have the potential to disperse to and inhabit pools year-round. Skimmer dragonflies only inhabit aquatic habitats during the nymph stage of their lifecycle which is often timed with season. Because *Pantala spp.* has temperature-sensitive egg development and does not overwinter in the nymph

stage like other odonates do we expect lower densities in the Spring compared to Summer and early Fall (Ichikawa et al. 2017).

We expected differences between each taxa's response to flooding. Specifically, we hypothesized that metrics representing high hydrologic connectivity including lower river flood heights, shorter distances to the river channel will have a positive influence on snail densities. We hypothesized that reduced flooding frequency (temporal isolation), measured as the number of days between when a pool was last inundated and sampling would be positively correlated with larval dragonfly densities. We also expected seasonal differences in mean dragonfly larvae densities because the aquatic life stage of *Pantala* is seasonally dependent. For both organisms we expected a positive relationship between patch size, measured as pools surface area and average depth, and observed densities. By observing differences in how the densities of these two taxa respond to riverine landscape characteristics we hope to gain insights into the mechanisms that drive spatial and temporal biodiversity patterns.

Methods

Study Site

We sampled a system of riverine rock pools on the south of Belle Isle on the James River in Richmond, Virginia (37°31'44.98" N, 77°27'9.14" W) (Fig. 1). The site is situated along the fall line where a rapid change in elevation contributes to an increase in water velocity and hydrologic erosion of the granite riverbed. Scouring of the granite bedrock by the river over time has formed hundreds of cylindrical shaped pools which often occur in areas of fast-flowing water in a variety of substrates (Mitchell and Lasswell 2018; Gagne). In 1905 the Virginia Electric

Power Company dammed a section of the James river diverting water away from the Southside of the island which exposed large sections of granite bedrock within the river channel. Embedded within the granite bedrock are hundreds of rock pools that provide habitat for a variety of aquatic organisms (Ren et al. 2016). Pools are isolated from the free-flowing channel at varying river heights creating spatial and temporal gradients of hydrologic connectivity. We have mapped 751 of these pools at this study site (Fig. 1).

Sampling Protocol

We collected 575 samples from 314 different rock pools over five years (2012, 2016-19) using a standardized protocol. We collected 24 samples in 2012, 28 in 2016, 53 in 2017, 227 in 2018, and 243 in 2019. To avoid bias we generated a random list of pools to sample each week. We measured and recorded each rock pool's surface area and average depth. Snails and dragonfly nymphs were collected using 15.2 x 12.1 cm aquatic dipnets. A total of 9 sweeps were used to sample the water column, sides, and bottom of each pool. Sweeps were a standardized length of 25 cm to ensure that a consistent volume of water was sampled across all pools in our dataset. We calculated the percentage of the volume sampled in each pool we surveyed as measure of sampling effort.

Flood Models and Distance to River Channel

We were interested in characterizing spatial and temporal connectivity of rock pools to the river including linear distance to the river channel, vertical distance above the channel, and time since inundation. Because of the small extent of our study site and our need for fine-grained and within-channel flood mapping data prevented us from using traditional modeling techniques.

We employed a novel approach to this problem by creating statistical models of river inundation for each pool using remote sensing, geographic information systems, USGS river gauge data, and logistic regression.

The first step in creating our models was to link water surface heights at our study site to a point of reference. In our models, we used upstream data provided by the USGS Westham gauge as our reference (Fig 2). The datum for this gauge is 98.82 feet above sea level (NGVD 29) and river heights provided by the gauge start at zero feet above this elevation. We used a DJI Mavic Pro 2, a commercially available unmanned aerial vehicle (UAV), fitted with a Hasselblad L1D-20c camera to obtain overhead images of our study site across a range of river heights corresponding to the upstream USGS gauge. Images of the study site were captured using Pix4DCapture (version 4.10.0) with a sensor angle of 90 degrees. We then generated orthomosaic images for each flight using Pix4DMapper (version 4.5.6).

When then imported the orthomosaic images into Esri's ArcGIS Pro (version 2.4) and we overlaid a point layer representing each mapped rock pool in our study system. The orthomosaic images were georeferenced to our point layer. For each image corresponding to a given river height we manually scored each pool with 1 for flooded or 0 for not flooded. We scored each pool for 17 different river heights ranging from 3.47-13.3 feet. Logistic regression was then used to model the probability of being flooded for a given river height for each pool in our system. The estimated flood height of a pool is the river height that corresponds to the inflection point (i.e. when the probability of flooding equals 0.5) of the logistic regression model. The data for many of our models exhibited complete separation which often causes parameter estimates to diverge to positive or negative infinity for traditional logistic models. To overcome this problem, we fit the models using Firth's biased reduced logistic regression using the brglm package in R (

Kosmidis 2019). We then calculated the number of days between flooding and the following

sampling event for each row in our dataset using flood heights extracted from the models, the

historical upstream gauge data, and the R programming language (R Core Team 2018).

Because the width and position of the channel is dependent on river discharge, we

measured distance to the river channel as the Euclidean distance between a pool and the position

of the river channel at its lowest stage height. We drew a polygon representing the river channel

at our study site using an orthophoto that corresponds to a river height of 3.47 feet at the

upstream gauge in ArcGIS Pro. We used this river height because it represents the initial position

of the free-flowing channel. We then used a shapefile of rock pool points to measure the distance

of each pool to the channel using the st_distance function in the R package sf (Pebesma and

Bivand 2005).

Data Analyses

We modeled snail and dragonfly nymph densities in pools as a function of flood height,

distance to the river channel, surface area, average depth, and season. We grouped month by

meteorological season with Spring including March, April, and May; Summer including June,

July, and August; Fall including September, October, and November; and Winter including

December, January, and February. Pools were only sampled between March and November so

season only includes three levels. We modeled this relationship using generalized linear mixed

models (GLMMs) using the R package glmmTMB (Brooks et al. 2017). The fixed effects in

each model included pool surface area (cm^3), the number of days between flooding and

sampling, pool flood height (ft), average depth (cm), distance to the river channel, and season.

To reduce the chances for type I and II errors because of non-independent data we included pool

and year as random effects in the models (Zuur and Ieno 2016). We scaled the covariates to a mean of 0 and a standard deviation of 1 so that the magnitude of coefficients represented their relative effect size within and between models (Schielzeth 2010). Prior to scaling we log-transformed surface area and average depth and used a log + 1 transformation on the covariate days between flooding and sampling. To reduce bias caused by increased sampling effort in smaller pools we added the percentage of water volume sampled as a scaled covariate in our models. For both models the percentage of the pool sampled was not a significant predictor of organism densities so we dropped the covariate from our final models. We checked for collinearity among covariates in the model using ggpairs function in the R package GGally (Schloerke et al. 2018).

We chose a non-Gaussian error structure to model organism densities. Because we modeled count data with a large percentage of zeros (snails = 68.3 %, dragonflies = 65.4 %) we fit models with a Poisson, Negative Binomial, and Zero Altered Poisson error distributions each with a log link function. We used Akaike's information criterion (AIC) to choose our error structure. For each GLMM the Negative Binomial error structure produced the most parsimonious models with the lowest AIC values, which we present in this paper.

The final models were checked for overdispersion using the DHARMa package in R (Hartig 2020). Additionally, ensure that models were not zero-inflated we simulated the models 10,000 times and compared the distribution of the percentage of simulated zeros to the actual percentages of zeros in the dataset.

We calculated a marginal pseudo r-squared value for each model using the performance package in R (Lüdecke et al. 2020; Nakagawa et al.). Graphical displays of the model outputs

were created using the dotwhisker, effects, and ggplot2 packages in R (Wickham 2016; Solt and Hu 2018).

Results

Rock pools at the study site varied in their flood height, distance from the free-flowing river channel, and size. Estimated rock pool flood heights ranged from 3.76 to 13.09 feet with a mean of 6.98 feet. The 95% confidence intervals around each flood height estimate ranged from 1.48 to 10.46 feet with an average of 2.82 feet. The widest confidence intervals were around the lowest and highest flood height. Additional UAV flights will increase the precision of these models. Pool distances from the river channel ranged from 0.42 to 101.23 meters and the mean distance was 32.73 meters. Of the pools sampled for snail and dragonfly densities, the mean surface area was 7,333.9 cm^3 with a mean depth of 31.28 cm. The number of days between flooding and sampling of a pool ranged from 0 to 223 days with a mean of 42.2 days. Mean densities of *Elimia virginica* and *Libellulidae* spp. differed between months (Fig. 3).

Pool connectivity and patch size determined snail densities. Increasing flood height had a strong negative effect on snail densities with a relative effect size of -0.68 (95% CI -0.99 to -0.38), i.e., pools that are connected to the river channel only at high water events supported fewer snails per volume than pools that are inundated at a lower river level. Surface area was an equally important in predictor in the model 0.66 (95% CI 0.45 to 0.87) with snail densities increasing with pool size. Snail densities decreased with increasing pool distance from the river channel -0.38 (95% CI -0.62 to -0.14) and average depth -0.24 (95% CI -0.46 to -0.02). Days between flooding and sampling -0.18 (95% CI -0.45 to 0.08) was of less importance when predicting snail densities in our model. We found no significant difference between snail

densities between seasons. The variance explained by the fixed effects of the GLMM of snail density, reported as pseudo R^2, was 0.265.

Dragonfly densities were determined by the amount of time pools were available for aerial colonization and season. An increase in the number of days between flooding and sampling positively influenced dragonfly nymph densities in our model 0.69 (95% CI 0.45 to 0.87). The relative effect size of this predictor was over seven times greater than all other coefficients in the model. Mean dragonfly larvae densities in rock pools were significantly lower in Spring than in Fall and Summer (Fig. 4). The variance explained by the fixed effects of the GLMM of dragonfly nymph density, reported as pseudo R^2, was 0.353.

Overall, we found that these two taxa responded to flooding and habitat characteristics as one might expect based on differences in their traits. The models of *Elimia virginica* and *Libellulidae* spp. densities showed differences in the magnitude and direction of coefficient estimates (Fig. 5). Surface area had a positive influence on both dragonfly nymph and snail densities, while flood height had a negative influence on their densities. However, the relative effect size of flood height in the snail model was 13 times greater than the dragonfly model and the coefficient for surface area in the snail model was 7 times greater than the dragonfly model. Dragonfly nymph densities increased as the number of days between flooding and sampling increased while snail densities decreased, and the absolute magnitude of the relative effect size was over 3.75 times greater in the dragonfly density model.

Discussion

The size of patches and the degree to which they are connected within a landscape influence important mechanisms that explain both species densities and richness. However,

responses to these landscape components could be dependent on species traits. Here we have shown how two taxa with different dispersal modes and life histories respond to hydrological connectivity, patch size, and season in a system of riverine rock pools.

We expected *Elimia virginica* and *Libellulidae spp* to respond differently to connectivity of the landscape, which is consistent with other studies (Gallardo et al. 2009). Our results indicate there are differences in how these two taxa respond to flooding. We found a strong negative effect of increasing flood height and distance from the river channel, two predictor variables associated with increased hydrologic connectivity, for snails while there was no effect on Libelluid dragonfly nymphs. Conversely, we observed a positive relationship of temporal isolation on dragonfly nymph densities while there was no effect on snail densities. This suggests snail densities in the landscape are not only dependent on distance from the river channel, but also hydrological connectivity associated with river pulses. Highly mobile dragonflies who disperse through the landscape and colonize pools via female oviposition show no directional pattern associated with river pulses but instead with increased temporal isolation. Differences in responses to connectivity could drive spatial heterogeneity of rock pool assemblages at the landscape scale. We found that *Elimia virginica* densities were not correlated with temporal isolation in rock pools. This observation coupled with the directional pattern of densities suggests that snails could be dispersal limited in this system. If other taxa are limited in their dispersal by distance from the river this could lead to spatial turnover of rock pool assemblages (Heino et al. 2015). Similarly, differences in responses among taxa to hydrological connectivity could drive patterns of temporal turnover of assemblages at the landscape scale. Larval dragonfly densities increased with temporal isolation while snails showed no correlation. These differences in response to connectivity could lead to shifts in community composition (Van Buskirk 1989).

We hypothesized that the densities of both taxa would increase with pool size. Interestingly snail densities were positively correlated with pool surface area and negatively with pool depth. This observation might be caused by differences in available resources driving increased colonization rates or by sustaining larger populations of snails. For example, there may be more periphyton in pools with larger surface area to depth ratios. We expected a positive correlation between larval dragonfly densities and patch size and other studies have found a positive relationship with pool size (Mitchell and Lasswell 2018; Gagne 2019). However, we found no relationship for this taxon for either metric of patch size (surface area and average depth). A potential explanation for our findings is that cannibalism in dragonfly nymphs is density-dependent (Van Buskirk 1989). If this is the case cannibalism could regulate nymph densities even when oviposition is higher in larger pools. Differences in response to patch size among taxa pre and post-colonization could also drive the spatial biodiversity of rock pool assemblages at the landscape scale.

Here we have shown how two taxa with different life histories and dispersal abilities respond to hydrological connectivity, patch size, and season in a system of riverine rock pools. Our study highlights how differences in response to these landscape characteristics are dependent on organism traits. These findings give insight into patterns of abundance and diversity across scales. We chose two taxa with broad differences in their dispersal abilities and life histories however, there are many organisms in this study system that share traits with these taxa. For instance, there are many taxa with complex life cycles including mosquitoes, damselflies, choronomids, and amphibians that colonize pools aerially or overland that we might expect to exhibit similar responses to riverine landscape characteristics as dragonflies. Similarly, we find many organisms inhabiting rock pools that can only access pools when they are inundated by the

river including other species of gilled snails, fish, and amphipods which might respond to hydrologic connectivity in ways that are analogous to those of the Virginia river snail. Given the potential responses of other organisms based on their traits we might expect spatial and temporal diversity patterns driven by landscape characteristics.

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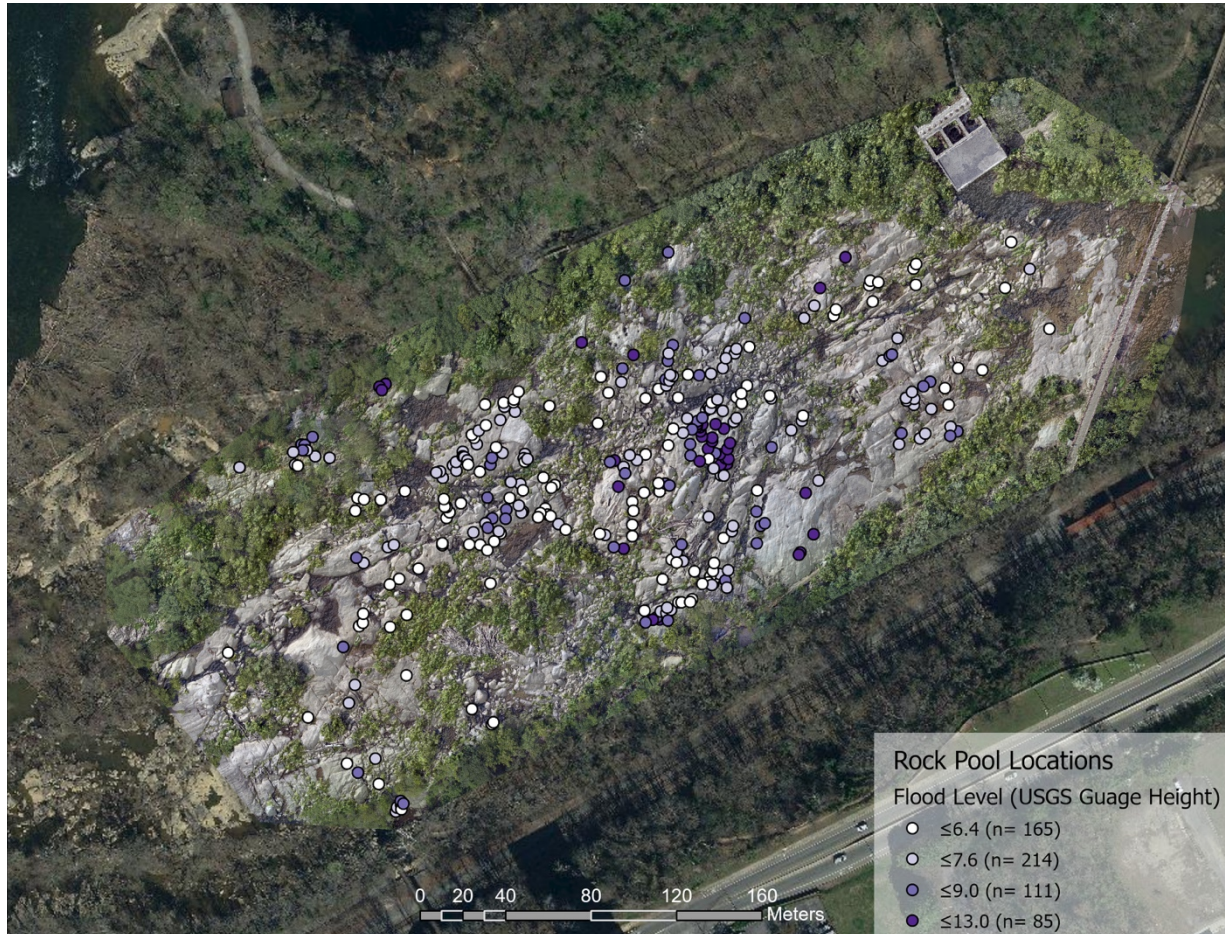
Figures

Fig. 1. A map of the rock pools on the south side of Belle Isle in the James River in Richmond, VA. Each point represents an individual rock pool (n = 314). The symbology of each point represents the stage height at the USGS gauge at Westham. Lighter points are flooded at lower river heights and darker point at higher river heights.

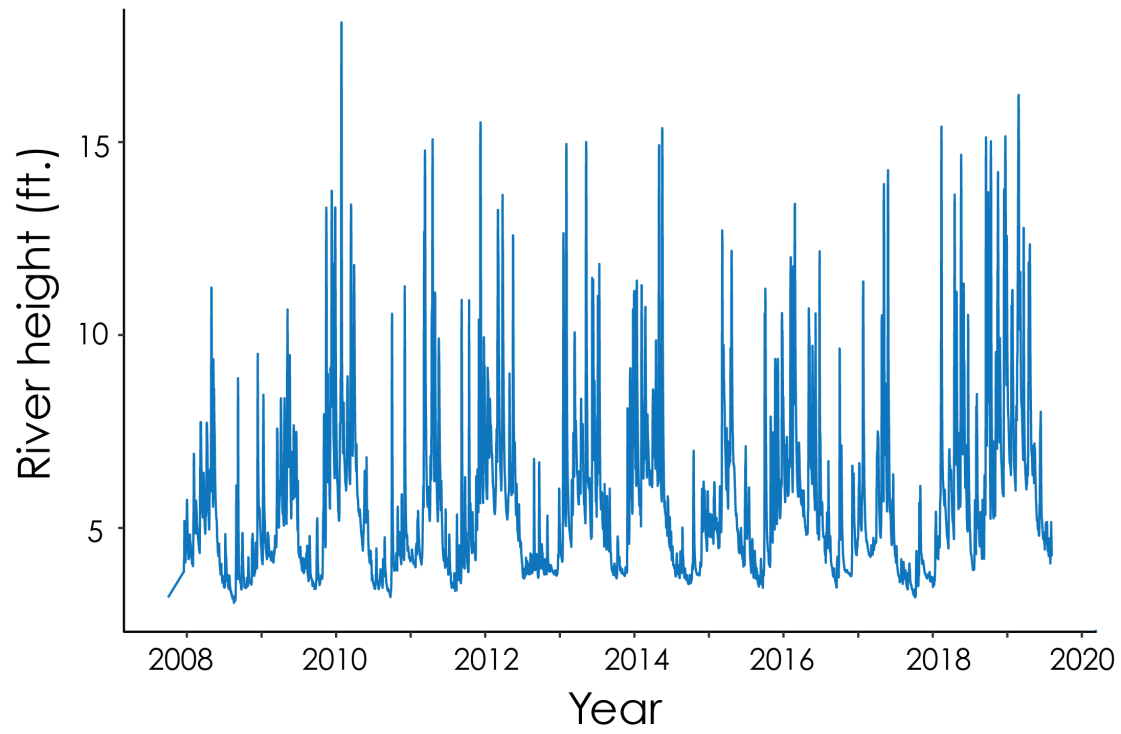**Fig 2.** River stage height of James River measured in feet collected from the USGS gauge at Westham.
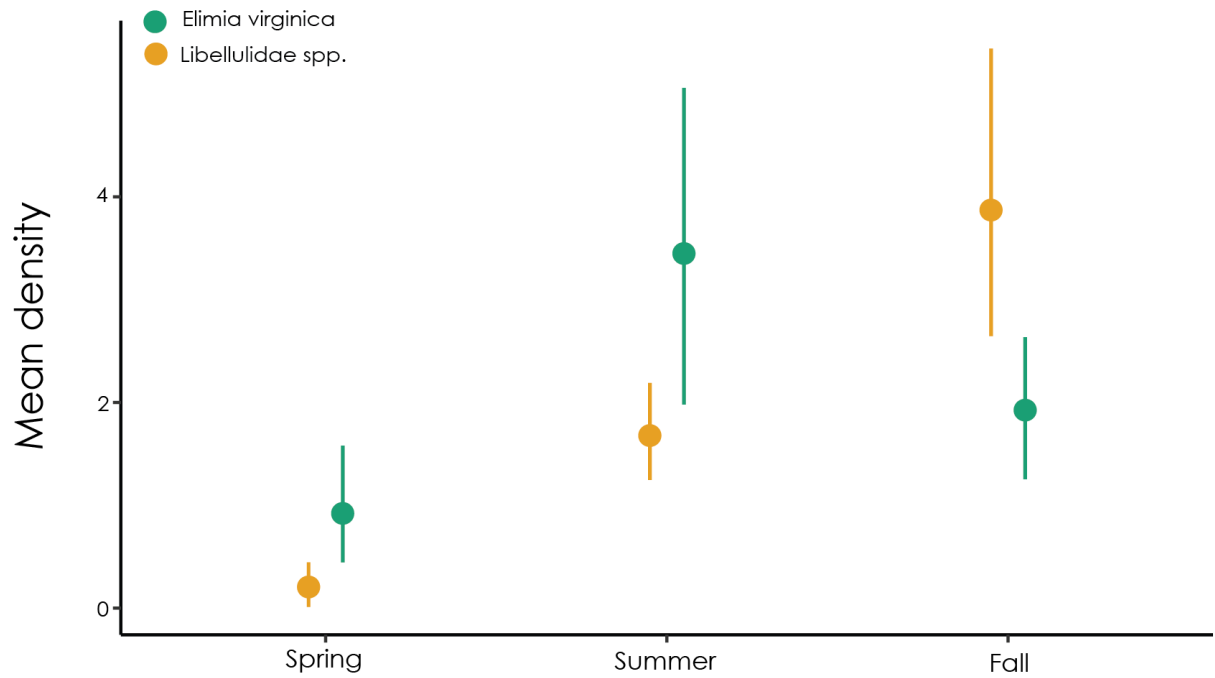
Fig 3. Mean densities of *Elimia virginica* and *Libelludae* spp. per season. Error bars represent bootstrap 95% confidence intervals.
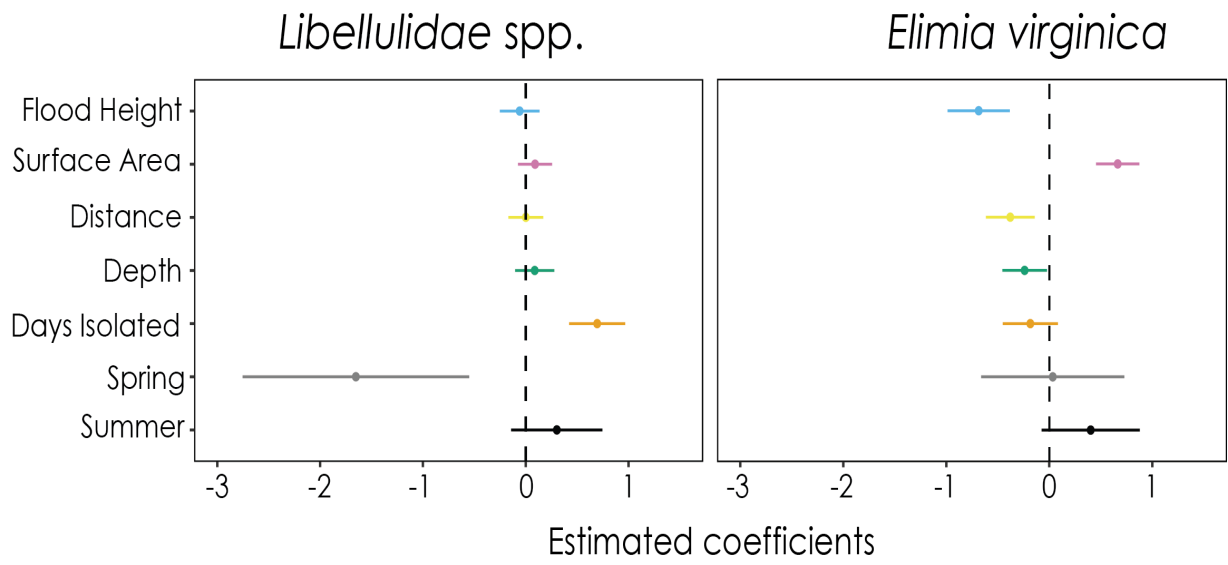
Fig. 4. Coefficients from the GLMMs modeling snail and dragonfly larvae densities. Covariates in the models were scaled with a mean of 0 and a standard deviation 1 so that represent their relative effect size in the model. Error bars represent 95% confidence intervals.
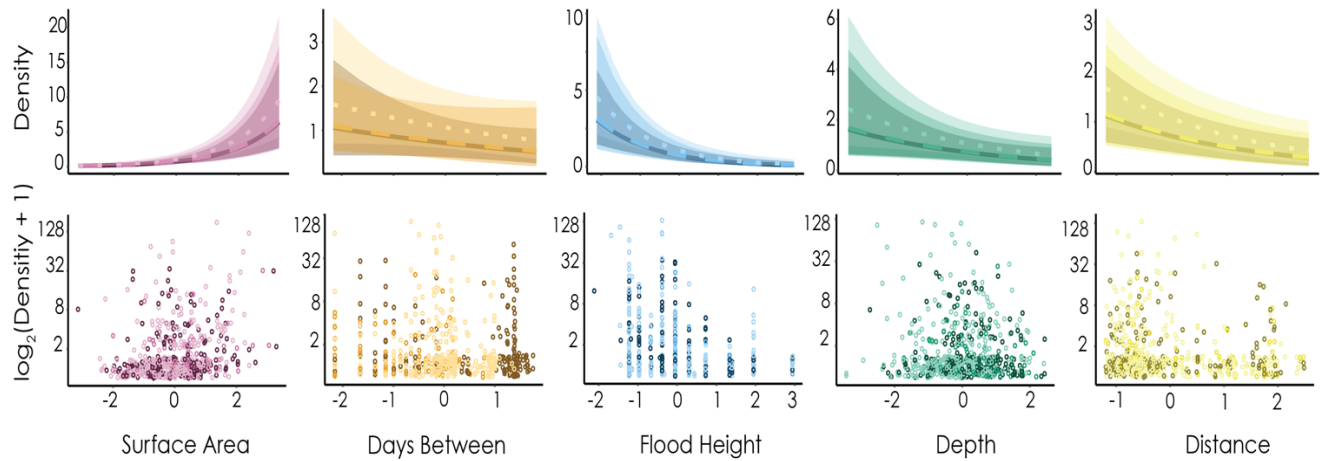
Fig. 5. Marginal effects plots from GLMMs modeling snail densities as a function of pool flood height, surface area, distance from the river channel, average depth, days between pool inundation and sampling, and surface area. Confidence intervals are 95%. Seasons are represented by color and line type with Fall represented by a solid line and darkest confidence interval, Spring a dotted line with an intermediate confidence interval, and Summer a dashed line with the lightest confidence interval.
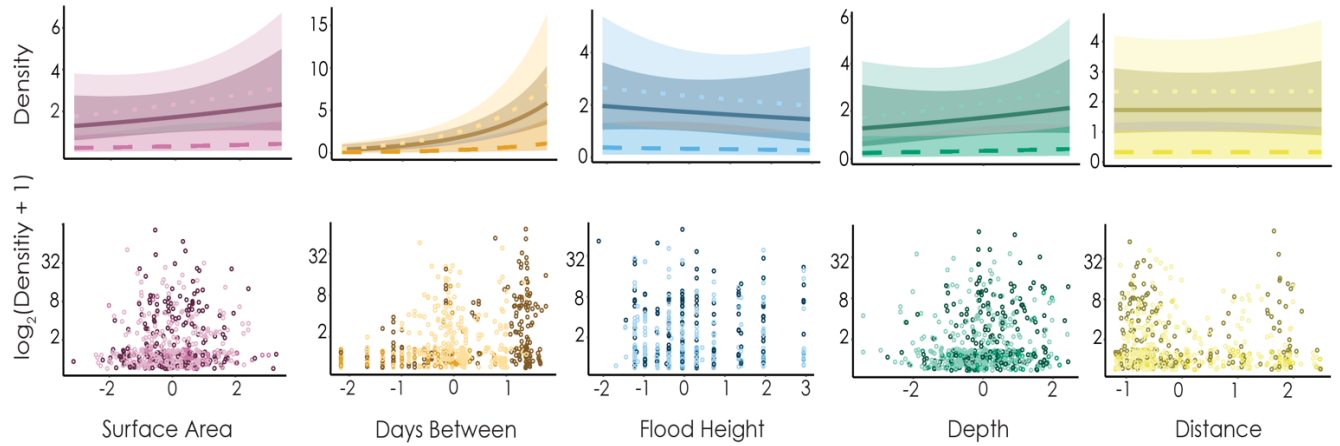
Fig. 6. Marginal effects plots from GLMMs modeling dragonfly nymph densities as a function of pool flood height, surface area, distance from the river channel, average depth, days between pool inundation and sampling, and surface area. Confidence intervals are 95%. Seasons are represented by color and line type with Fall represented by a solid line and darkest confidence interval, Spring a dotted line with an intermediate confidence interval, and Summer a dashed line with the lightest confidence interval.

Vita

Charles Ryland Stunkle was born April 1st, 1982 in Fredericksburg, VA. He graduated in 2018 from Virginia Commonwealth University with a Bachelor of Science in Environmental Studies. He began graduate studies in 2018 and received a Master of Science in Environmental Studies degree in 2020.