Taxa-specific responses to flooding shape patterns of abundance in river rock pools

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Abstract: Connectivity and patch size 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 the densities of 2 taxa that differ in life history and dispersal ability, the Virginia River Snail (*Elimia virginica*) and skimmer dragonfly larvae (*Pantala* spp.), as a function of flooding, patch area, and season in >300 riverine rock pools. We found key differences in how each taxon responded to these predictors. Specifically, increasing pool flood height had a strong negative effect on snail densities, whereas dragonfly nymph densities increased as pools became isolated from the river channel for longer durations of time. Increasing pool surface area had a positive effect on snail densities, whereas dragonfly nymph densities showed no such relationship. Dragonfly nymph densities were greater in summer and autumn than in spring, but snails showed no difference in their temporal distribution across seasons. Our study highlights how differential responses to landscape characteristics are dependent on organism traits. These findings give insight into patterns of abundance and diversity across spatiotemporal scales.

Key words: rock pool, abundance patterns, riverine landscapes, hydrologic connectivity

Connectivity and patch size are critical components of landscape structure (Godron 1981, Taylor et al. 1993) because they underpin key processes that determine species abundance and richness across scales (Simberloff and Wilson 1969, Hanski 1999, Leibold et al. 2004). More connected habitats typically have higher dispersal and colonization rates, which lead to greater species persistence, gene flow, and movement of energy and matter within a landscape (Fahrig and Merriam 1985, Tockner et al. 1999, Keyghobadi et al. 2005, Frisch et al. 2012, Thompson et al. 2017). Patch size also influences population densities and species richness (Hill et al. 1996, Bender et al. 1998, Connor et al. 2000, Matter 2000, Schuler et al. 2017). Consequently, habitat fragmentation is often a contributing factor to declines in biodiversity, which highlights the need to improve our understanding of 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 the life histories of organisms could lead to asymmetric responses among species to landscape patchiness and connectivity. For instance, highly vagile species may be less sensitive to low habitat connectivity compared to less mobile organisms (With and Crist 1995, D'Eon et al. 2002). Likewise, there are disparities in responses to patch size that are associated with differing species traits (Steffan-Dewenter and Tscharntke 2000, Prugh et al. 2008). Differential responses among species to landscape connectivity and patch size ultimately shape spatial and temporal patterns of abundance and diversity at the local and landscape scales. In periodically connected ecosystems, such as riverine floodplains, different traits and life histories of species

can drive changes in community structure over space and time (Robinson et al. 2002).

In this paper, we focus on periodic connectivity between habitat patches in riverine floodplains that occurs via pulses of river discharge into surrounding terrestrial habitats (Tockner et al. 2000). Specifically, we focus on the lateral and temporal dimensions of hydrologic connectivity (Ward 1989, Amoros and Bornette 2002) to explore how connectivity, patch size, and season influence densities of 2 taxa with different life histories and dispersal abilities in a system of periodically flooded riverine rock pools. Pools are well suited for this research because they can be numerous, vary in size, and are easily sampled. Moreover, the spatial and temporal connectivity of rock pools can be rigorously quantified. Pools vary in their distance from and height above the river channel creating a gradient of lateral hydrological connectivity depending on the river's flood stage.

For this study, we leveraged data collected over 3 y to model the densities of dragonfly nymphs (*Pantala* spp. Hagen, 1861; Libellulidae) and Virginia River Snails (*Elimia virginica* Say, 1817; Pleuroceridae). We chose these taxa for comparisons because they have life histories and traits representing the extremes of the hydrologic connectivity spectrum. The dragonflies in this study often carry out the nymph stage of their life cycle in temporary water bodies, such as ephemeral ponds and rain pools (Tennessen 2019). Therefore, we expected higher colonization by dragonflies via adult oviposition into pools during periods of low hydrologic connectivity. In contrast, when hydrologic connectivity is low, snail movement is restricted as pools become isolated from the river. Conversely, when lateral connectivity is high, snails are able to colonize and move between rock pools. Following colonization, we expected asymmetric responses to flooding between these 2 species. The Virginia River Snail 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 as dragonfly nymphs, which oviposit in lentic freshwater habitats. Therefore, we expected densities of dragonfly nymphs to increase with pool temporal isolation (i.e., the amount of time since the pool was last inundated by the river) and densities of snails to decrease. For both taxa, we expected increased resources associated with larger pool size to sustain higher densities following colonization. By analyzing differences in how the densities of these 2 taxa respond to riverine landscape characteristics, we hope to gain insights into the mechanisms that drive spatial and temporal biodiversity patterns.

METHODS

To address our research question of how hydrologic connectivity, patch size, and season influence the abundances of taxa with different life histories and modes of dispersal, we conducted a field study over 3 y in which we sampled aquatic macroinvertebrates in a complex system of riverine rock pools in Richmond, Virginia, USA. Specifically, we modeled the densities of *E. virginica* and *Pantala* spp. as a function of pool flood height (m), surface area (cm^2), depth (cm), distance to the river channel (m), the number of days between flooding and sampling, and season.

Study site

We sampled a system of 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 Atlantic Seaboard 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 various substrates (Ortega et al. 2014, Pelletier et al. 2015) and provide habitat for a variety of aquatic organisms (Ren et al. 2016). In 1905, the Virginia Electric Power Company dammed a section of the James River, diverting water away from the south side of the island and exposing large sections of granite bedrock within the river channel. The study site at Belle Isle covers an area of 0.06 km^2 and contains 751 pools that were identified and mapped prior to this study (Jackson 2010). Pools are isolated from the free-flowing channel at varying river heights, creating spatial and temporal gradients of hydrologic connectivity. Because of the study site's topography, these gradients can occur over relatively short distances. For example, pools 246 and 681 are separated by a distance of 18.6 m, but they are flooded at river stage heights of 3.43 and 1.65 m, respectively (Fig. 1). During the years we sampled, the pool at 3.43-m flood height flooded an average of 18.7 d/y, whereas the pool at 1.65-m flood height flooded an average of 162.7 d/y, almost a 9× difference in the average number of days flooded over a distance of 18.6 m. This disparity in flood heights leads to differences in the frequency and duration of flooding each rock pool experiences within a given period (Fig. 2 A–C).

Sampling protocol

We collected 523 samples from 302 different rock pools over 3 y (2017–2019) using a standardized protocol. We collected 53 samples in 2017, 227 in 2018, and 243 in 2019. To avoid bias, we sampled randomly selected pools during each sampling event. We used a Rigid No. 1602 ruler (Rigid Tool Company, Elyria, Ohio) to measure the surface area of each rock pool and their depths at 4 random points from which we calculated mean depths. We collected snails and dragonfly nymphs with aquarium dipnets, and we used a reference collection to identify and enumerate all organisms in the field. The reference collection consisted of organisms preserved in ethanol and identified to the lowest taxonomic level in the lab (Peckarsky et al. 1993, Tennessen 2019). Both species of *Pantala* nymphs, *Pantala flavescens* (Fabricius,
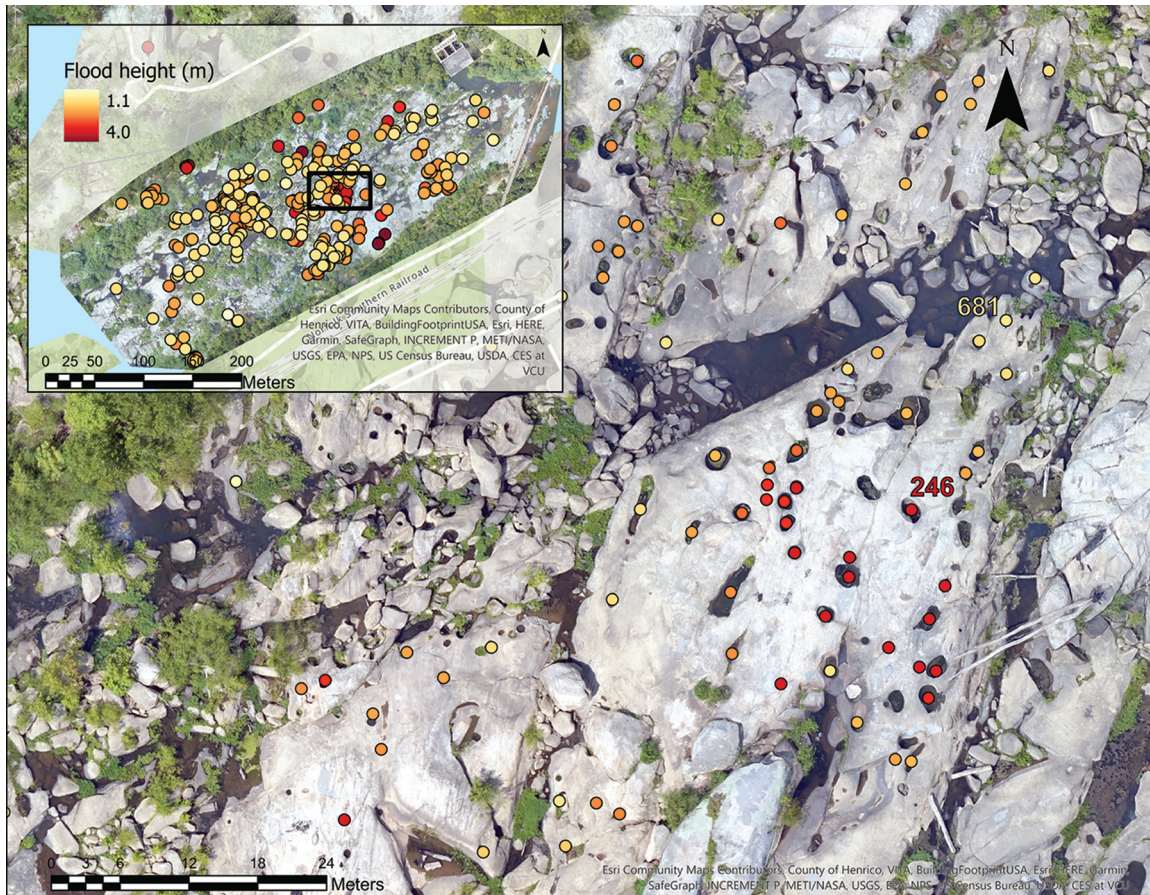
Figure 1. A map of the rock pools on the south side of Belle Isle in the James River in Richmond, Virginia, USA. Each point represents an individual rock pool that we sampled during the study ($n = 302$). The inset map shows the entire study site, and the main portion of the map displays a detailed section of the site. The symbology of each point represents the stage height at the upstream United States Geological Survey Richmond-Westham gauge. Lighter points are flooded at lower river heights and darker point at higher river heights. Pools 246 and 681 are labeled to highlight the gradient of pool flood height described in the manuscript text.

1798) and *Pantala hymenaea* (Say, 1839), are found in pools at our study site; however, genus was the lowest reliable taxonomic level we could identify for dragonfly nymphs in the field. We used a total of 9 dipnet sweeps to sample the water column, sides, and bottom of each pool. Sweeps were a standardized length of 25 cm and made with 15.2×12.1-cm aquarium dipnets to ensure that we sampled a consistent volume of water 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 created and verified (using drone imaging) a flood model for each pool in our study system to estimate a pool's hydrologic connectivity over time. We characterized the spatial and temporal connectivity of rock pools based on their linear distance to the river channel (m), vertical distance above the channel (m), and time since inundation (d). Because of the small extent of our study site and our need for fine-grained and within-channel flood mapping data, we

developed a novel approach using statistical models of river inundation for each pool based on remote sensing, geographic information systems, United States Geological Survey (USGS) river gauge data, and logistic regression.

The 1st 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 Richmond-Westham gauge as our reference, which is vertically surveyed at 30.12 m a. s. l. (NGVD 29) (Fig. 2A). For our study, river heights provided by the USGS gauge start at 0 m above this elevation, so we have a consistent and stable vertical benchmark to measure flooding downstream in our study area.

We created on-demand orthophotos of our entire study area by using a Mavic Pro 2 (DJI, Shenzhen, China), a commercially available unmanned aerial vehicle (UAV) fitted with a Hasselblad L1D-20c camera (Gothenburg, Sweden). We used Pix4Dcapture (version 4.10.0) to create a reproducible flight plan for the UAV to follow, and we collected geotagged images of our study site across a range of river heights (16 total
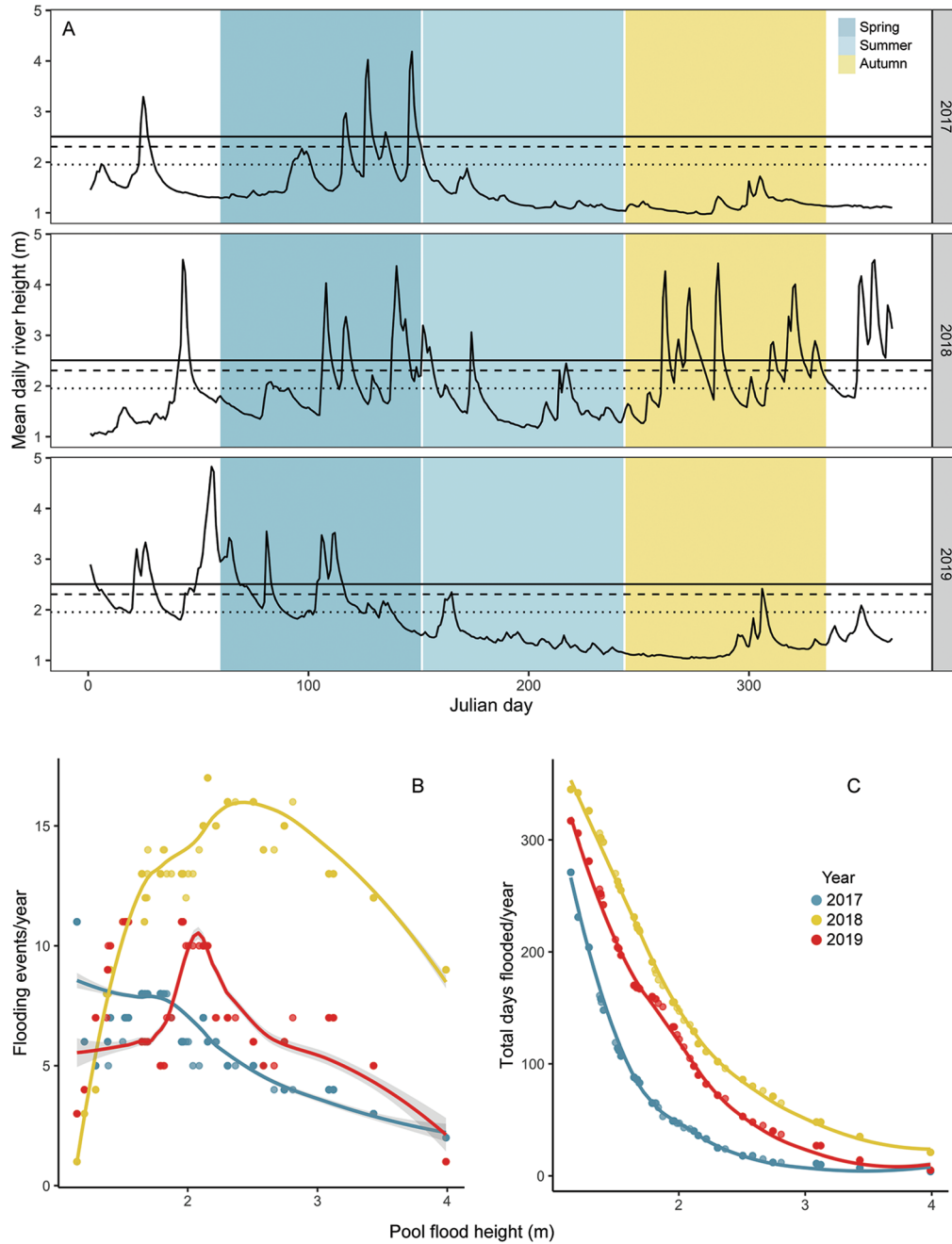
Figure 2. River stage height (m) of the James River in Richmond, Virginia, USA, collected from the upstream United States Geological Survey Richmond-Westham gauge, with horizontal lines representing stage heights at which 25% (dotted line), 50% (dashed line), and 75% (solid line) of pools at the study site are flooded (A); estimated number of pool flooding events/year (B); and the total number of days each pool was flooded/year (C). In panels B and C, lines represent smoothed conditional means, and gray shaded areas represent 95% confidence intervals.

flights) corresponding to the upstream USGS gauge. Images of the study site were captured at nadir (90°) for horizontal mapping. We used Pix4Dmapper (version 4.5.6) to create a digital elevation model, digital surface model, and orthophoto from the geotagged images collected during each flight.

We imported the resulting orthomosaic images into ArcGIS Pro (version 2.4; Esri™, Redlands, California) and 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 then used logistic regression 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 = 0.5) of the logistic regression model. The data for many of our models exhibited complete separation, which often causes parameter estimates in traditional logistic models to diverge to positive or negative infinity. To overcome this problem, we fit the models using Firth's biased reduced logistic regression using the *brglm* package (version 0.6.2; Kosmidis 2019) in R (version 4.0.4; R Project for Statistical Computing, Vienna, Austria). We then calculated the number of days between flooding and the following sampling event for each pool in our dataset using flood heights extracted from the models, the upstream USGS gauge data, and the R programming language.

Because the width and position of the main river 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. In ArcGIS Pro, we drew a polygon representing the river channel at our study site by using an orthophoto that corresponded to a river height of 1.06 m at the upstream gauge. 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 by using the st_distance function in the R package *sf* (Pebesma 2018).

Data analyses

Using a separate model for each taxon, we modeled snail and dragonfly nymph densities as a function of pool connectivity, patch size, and season. We grouped month by meteorological season with spring including March, April, and May; summer including June, July, and August; autumn including September, October, and November; and winter including December, January, and February. We only sampled pools between March and November, so the winter months were excluded from our analysis. We modeled the relationship between the predictor variables and the densities of snail and dragonfly nymphs by using generalized linear mixed models (GLMMs) in the R package *glmmTMB* (Brooks et al. 2017). The fixed effects in each model included pool surface area (cm^2), the number of days between flooding and sampling, pool flood height (m), mean depth (cm), distance to the river channel (m), 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 continuous 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 mean depth and used a log + 1 transformation on the number of days between flooding and sampling to improve homoscedasticity. To ensure there was no bias caused by increased sampling effort in smaller pools, we created separate models with the addition of percentage of water volume sampled as a scaled covariate. The percentage of the water volume sampled was not a strong predictor of snail densities (effect size: −0.03; 95% confidence interval [CI]: −0.41–0.35) or dragonfly densities (effect size: −0.04; 95% CI: −0.37 to 0.29), so we excluded that covariate in the models we present here. We checked our models for multicollinearity (collinearity between covariates) by calculating their variance inflation factor values using the check_collinearity function in the *performance* package (Lüdecke et al. 2020) in R. For both models, the variance inflation factor values of each predictor were no greater than 1.51, indicating low correlation between predictors.

Snail and dragonfly count data had a large percentage of zeros (snails = 68.3%, dragonflies = 68.3%); therefore, we compared models that assumed Poisson, negative binomial with a quadratic mean–variance relationship, and 0-altered Poisson error distributions, each with a log link function, by using Akaike's information criterion. For both snail and dragonfly nymph densities, models with negative binomial error structures had the lowest Akaike's information criterion values and are the basis for inferences in the remainder of this paper. We evaluated the final models for overdispersion by using the *DHARMa* package (version 0.3.3.0; Hartig and Lohse 2020) in R and via posterior simulations to determine if the observed percentage of zeros in our data deviated from expectations of the fitted model and found no evidence of overdispersion in the models we present. We calculated a marginal pseudo R^2 value for each model by using the *performance* package in R (Nakagawa et al. 2017). We created graphical displays of the model outputs by using the *dotwhisker* (version 0.6.0; Solt et al. 2018), *effects* (Fox and Weisberg 2019), *wesanderson* (version 0.3.6; Karthik et al. 2018), and *ggplot2* (Wickham et al. 2016) packages in R.

RESULTS

Rock pools at the study site varied in their flood height, distance from the free-flowing river channel, and size (surface area and mean depth). Estimated rock pool flood heights ranged from 1.15 to 3.99 m, with a mean of 2.32 m. Pool distances from the river channel ranged from 0.42 to 101.23 m, with a mean distance of 33.41 m, which resulted in large variation in the frequency and duration of inundation of pools. The mean number of flooding events/y ranged from 4 to 11 occurrences during the years that we sampled, with a mean frequency of 8.86 occurrences/y (Fig. 2B). Similarly, the mean number of days pools spent inundated by the river/y ranged from 10 to 311 d, with a mean of 109.1 d (Fig. 2C). Of the pools sampled for snail and dragonfly densities, the mean surface
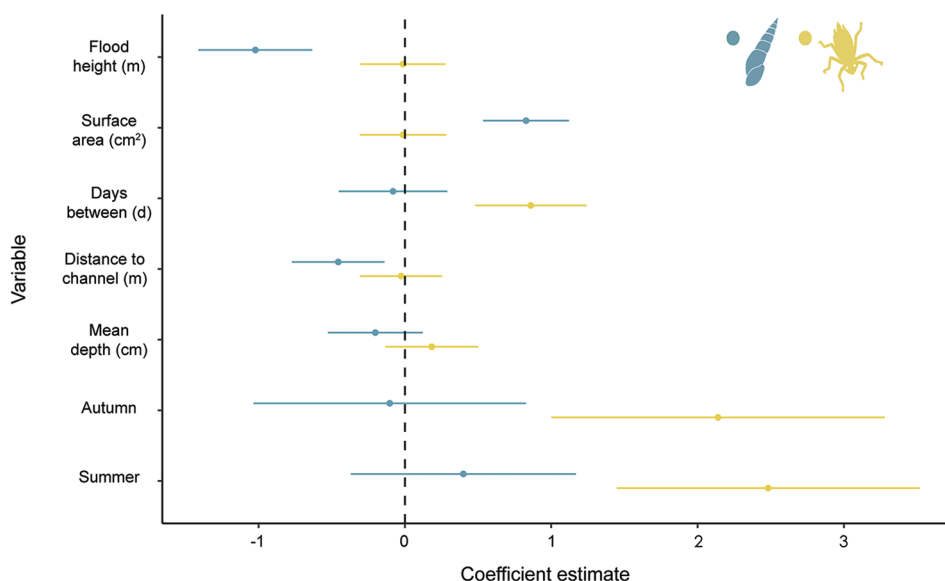
Figure 3. Coefficients from the generalized linear mixed models modeling snail (blue dark closed circle) and dragonfly larvae (yellow closed circle) densities (ind./pool). Spring is the reference category for each model presented. Continuous variables in the models were scaled with a mean of 0 and a standard deviation 1 so that they represent their relative effect size in each model. Error bars represent 95% confidence intervals. Flood height = river height at which a pool floods corresponding to the upstream gauge, Surface area = pool surface area, Days between = the number of days between when a pool was last flooded and when it was sampled, Distance to channel = pool distance to the river channel.

area was 7519 cm^2, and the mean depth was 30.28 cm. The number of days between flooding and sampling of a pool ranged from 0 to 200 d, with a mean of 37.8 d.

Pool connectivity and patch size determined snail densities (Figs 3, Fig. 4A). Increasing flood height had a strong negative effect on snail densities, with a relative effect size of −1.02 (95% CI: −1.41 to −0.63), i.e., pools that are connected to the river channel only at high water events supported fewer snails/volume than did pools that are inundated at a lower river level. Surface area was also an important predictor in the model, with an effect size of 0.83 (95% CI: 0.53–1.12) and snail densities increasing with pool size. Snail densities decreased with increasing pool distance from the river channel (effect size: −0.46; 95% CI: −0.77 to −0.14). Days between flooding and sampling (effect size: −0.08; 95% CI: −0.45–0.29) and mean depth (effect size: −0.20; 95% CI: −0.53–0.12) were of no importance when predicting snail densities in our model. We found no substantial difference in snail densities between seasons. Estimates for the random effects year and pool were 0.82 (95% CI: 0.31–2.19) and 1.43 (95% CI: 1.09–1.87), respectively. The variance explained by the fixed effects of the GLMM of snail density, reported as pseudo R^2, was 0.340.

Dragonfly densities were determined by the amount of time pools were available for aerial colonization and season (Fig. 4B). An increase in the number of days between flooding and sampling positively influenced dragonfly nymph densities in our model (effect size: 0.86; 95% CI: 0.48–1.24). The

relative effect size of this predictor was nearly 5× greater than that of all other scaled coefficients in the model. Mean dragonfly larvae densities in rock pools were greater in summer and autumn than in spring (Fig. 3). Estimates for the random effects year and pool were 0.32 (95% CI: 0.07–1.38) and 0.99 (95% CI: 0.70–1.42), respectively. The variance explained by the fixed effects of the GLMM of dragonfly nymph density, reported as pseudo R^2, was 0.424.

DISCUSSION

The size of patches and the degree to which they are connected within a landscape are strong predictors of both species' densities and richness. However, responses to these landscape components may depend on species traits. Here we examined differences in the responses of 2 taxa with dissimilar dispersal modes and life histories to hydrological connectivity, patch size, and season in a system of riverine rock pools. We found that *E. virginica* and *Pantala* spp. respond differently to connectivity of the landscape. Specifically, increasing flood height and distance from the river channel (indicating decreased hydrologic connectivity) had strong negative effects on snail abundances but no detectable effects on dragonfly nymphs. Conversely, we observed a positive relationship between temporal isolation (i.e., number of days between flooding and sampling) and dragonfly nymph densities, although this variable had no detectable effect on snail densities. These differences in responses to connectivity could drive spatial heterogeneity of rock pool
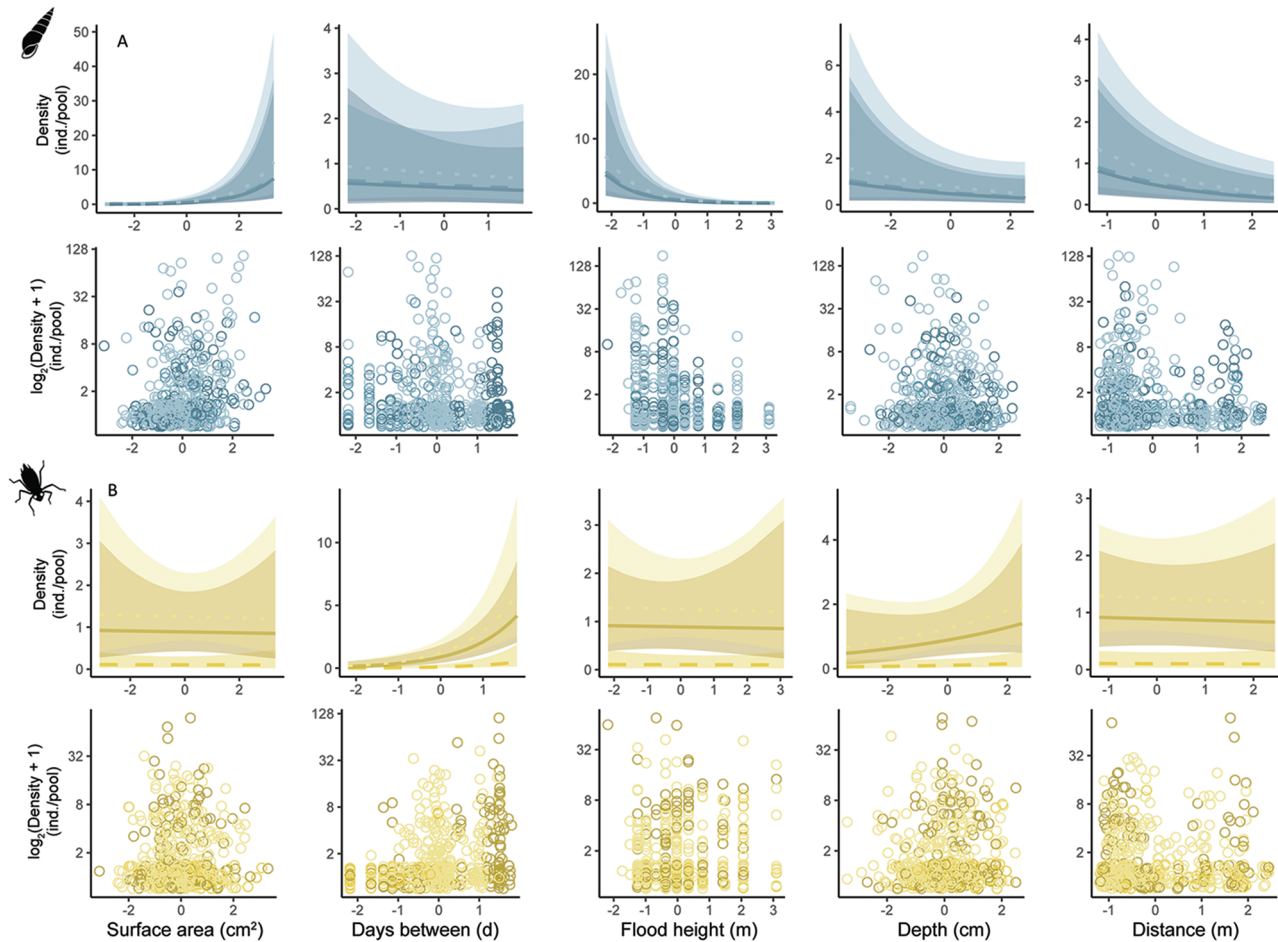
Figure 4. Marginal effects plots from generalized linear mixed models modeling larval dragonfly densities (ind./pool) (A) and snail densities (B) as a function of pool surface area, days between pool inundation and sampling, pool flood height, mean pool depth, and distance from the river channel. Shaded areas represent 95% confidence intervals. Seasons are represented by shading and line type with autumn represented by a solid line and the most darkly shaded confidence interval, spring a dashed line with an intermediately shaded confidence interval, and summer a dotted line with the most lightly shaded confidence interval.

assemblages in individual pools and at the landscape scale. The lack of temporal isolation effects coupled with the directional pattern of densities suggests that snails could be dispersal limited in this system. Conversely, highly mobile dragonflies, which disperse through the landscape and colonize pools via oviposition, showed no directional pattern associated with river pulses, but instead their densities increased with the number of days since pool flooding. If some taxa in this system are dispersal limited by hydrologic connectivity and others are not, then we might expect predictable spatial turnover of rock pool assemblages, and if organisms have dissimilar responses to temporal isolation, then we might expect temporal turnover of assemblages based on hydrodynamic characteristics of the system (Heino et al. 2015). For example, we might expect rock pool assemblages to shift from lotic organisms following flooding to lentic organisms as pools become isolated temporally from the river.

We hypothesized that the densities of both taxa would be positively correlated with pool size, but we found mixed results regarding this relationship. Interestingly, snail densities were positively correlated with pool surface area and there was no relationship between pool depth and snail densities. This observation might be due to differences in available resources driving increased colonization rates or 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 dragonfly nymph densities and patch size as demonstrated by other studies (Mitchell and Lasswell 2018, Gagne 2019), but we found no such relationship for this taxon for either metric of patch size (surface area or mean depth). One explanation for our findings is that cannibalism in dragonfly nymphs is density dependent (Van Buskirk 1989) and so these populations may be self-regulating nymph densities,

offsetting any increase in oviposition associated with larger pools. Oviposition behavior of *Pantala* spp. could also explain the lack of relationship between dragonfly density and pool size. Schenk et al. (2004) observed *P. flavescens* randomly ovipositing across all available pools in what the authors describe as spatial risk spreading.

We observed a difference in the temporal distributions of snails and dragonfly nymphs in our study that could be explained by the life histories of the organisms. Dragonfly nymph densities were higher in summer and autumn than in spring, a pattern possibly related to migration. Both species of *Pantala* are nomadic with migratory events often timed with seasonal rainfall, which would explain the temporal distributions we observed (Corbet 1999). An additional explanation for the seasonal patterns of dragonfly densities is that egg development of *P. flavescens* is temperature sensitive, and they do not overwinter in the nymph stage (Ichikawa et al. 2017). By contrast, we observed no substantial differences in snail densities between seasons. An explanation for this pattern is that Virginia River Snails are estimated to have lifespans of several years; therefore, they have the potential to disperse to and inhabit pools year round.

We focused on 2 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 or that may lie somewhere in between these 2 extremes. For instance, there are many other taxa with traits similar to those of *Pantala* spp., such as mosquitoes, damselflies, chironomids, and amphibians, which exhibit complex life cycles and colonize rock pools aerially or overland (Duchet et al. 2017). Flooding may have similar consequences for these organisms, e.g., flushing their larvae out of individual pools and into surrounding lotic habitats that are less suitable for their survival and development. However, the consequences of flooding for these species may depend on the duration of their larval development. For example, larvae of *P. hymenaea* and *P. flavescens* require a minimum of 28 and 43 d, respectively, to develop (reviewed in Corbet 1999, p. 630). By contrast *Aedes atropalpus* (Coquillett, 1902), a rock pool mosquito, can develop in ¼ of that time, whereas amphibians such as the American Toad (*Anaxyrus americanus americanus* Holbrook, 1836) require longer development times (Wright and Wright 1949, Day et. al 2020). Therefore, pools with shorter hydroperiods may be unsuitable habitat for some species but not others, depending on whether there is sufficient time for the larvae to complete development. 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 potentially similar responses of other organisms based on their shared traits, we might expect that the spatial and temporal connectivity of individual habitats might be a strong predictor of spatial and temporal diversity patterns.

We have shown how hydrologic connectivity, patch size, and season influence the abundance of snails and dragonfly nymphs in a system of rock pools. However, there are a number of biotic and abiotic factors that control community structure and the abundances of organisms in riverine landscapes (Tockner et al. 2000, Robinson et al. 2002). The models presented here explain <50% of the variation in snail and dragonfly nymph densities, suggesting there may be other important factors influencing the abundances of these organisms. For example, environmental gradients, such as in temperature and dissolved oxygen, as well as the presence of predators and competitors might partially explain the distribution of snails and dragonfly nymphs within the landscape (Wellborn et al. 1996). Future work in this system should include these predictors to determine the degree to which they influence organismal abundances and community structure.

Here we have shown how 2 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 responses to these landscape characteristics are dependent on the organisms' dispersal abilities and life-history traits and how these differences can lead to asymmetrical responses to landscape patchiness and connectivity. Additionally, these findings give insight into how periodic changes in habitat conditions and connectivity can drive patterns of abundance through time and across habitats. Given that habitat connectivity is defined by species traits interacting with environmental conditions, we might expect that, at the landscape scale, greater biodiversity is maintained when patches experience varying levels of spatial and temporal connectivity. This pattern may be particularly the case in ecotonal communities where this heterogeneity may enable species from different source habitats to persist.

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DATA SHARING

E-mail CRS for access to the Github repository containing all code used for the analyses and creation of figures presented in this manuscript.

LITERATURE CITED

Amoros, C., and G. Bornette. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshwater Biology 47:761–776.

Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology 79:517–533.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. *GlmmTMB* balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400.

Connor, E. F., A. C. Courtney, and J. M. Yoder. 2000. Individuals–area relationships: The relationship between animal population density and area. Ecology 81:734–748.

Corbet, P. 1999. Dragonflies: Behavior and ecology of Odonata. 3rd edition. Cornell University Press, Ithaca, New York.

D'Eon, R. G., S. M. Glenn, I. Parfitt, and M.-J. Fortin. 2002. Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conservation Ecology 6:10.

Day, C. A., E. G. Armstrong, and B. D. Byrd. 2020. Population growth rates of *Aedes atropalpus* (Diptera: Culicidae) are depressed at lower temperatures where *Aedes japonicus japonicus* (Diptera: Culicidae) are naturally abundant in rock pools. Journal of Medical Entomology 58:493–497.

Duchet, C., G. M. Moraru, O. Segev, M. Spencer, A. G. Hayoon, and L. Blaustein. 2017. Effects of flash flooding on mosquito and community dynamics in experimental pools. Journal of Vector Ecology 42:254–263.

Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival: Ecological archives E066-008. Ecology 66:1762–1768.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression. 3rd edition. Sage, Thousand Oaks, California.

Frisch, D., K. Cottenie, A. Badosa, and A. J. Green. 2012. Strong spatial influence on colonization rates in a pioneer zooplankton metacommunity. PLoS ONE 7:e40205.

Fuller, M. R., M. W. Doyle, and D. L. Strayer. 2015. Causes and consequences of habitat fragmentation in river networks: River fragmentation. Annals of the New York Academy of Sciences 1355:31–51.

Gagne, C. R. 2019. Spatial and temporal variation in the aquatic invertebrate community structure of rock pools along the Penobscot River, Maine. Master's Thesis. University of Maine, Orono, Maine.

Godron, M. 1981. Patches and structural components for a landscape ecology. BioScience 31:733–740.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A.O. Nicholls, J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87:209–219.

Hartig, F., and L. Lohse. 2020. *DHARMa*: Residual diagnostics for hierarchical (multi-level/mixed) regression models. (Available from: https://CRAN.R-project.org/package=DHARMa)

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, and L. M. Bini. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. Freshwater Biology 60:845–869.

Hill, J. K., C. D. Thomas, and O. T. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by hesperia comma butterflies: Implications for metapopulation structure. The Journal of Animal Ecology 65:725–735.

Ichikawa, Y., T. Yokoi, and M. Watanabe. 2017. Thermal factors affecting egg development in the wandering glider dragonfly, *Pantala flavescens* (Odonata: Libellulidae). Applied Entomology and Zoology 52:89–95.

Jackson, C. 2010. Factors influencing macroinvertebrate diversity and community composition in riverine freshwater rock pools. Master's Thesis. Virginia Commonwealth University, Richmond, Virginia. (Available from: https://doi.org/10.25772/0TE1-F239)

Karthik, R., H. Wickham, C. Richards, and A. Baggett. 2018. *wesanderson*: A Wes Anderson palette generator. (Available from: https://CRAN.R-project.org/package=wesanderson)

Keyghobadi, N., J. Roland, and C. Strobeck. 2005. Genetic differentiation and gene flow among populations of the alpine butterfly, *Parnassius smintheus*, vary with landscape connectivity: Landscape connectivity and gene flow. Molecular Ecology 14:1897–1909.

Kosmidis, I. 2019. *brglm*: Bias reduction in binomial-response generalized linear models. (Available from: https://cran.r-project.org/package=brglm)

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Lüdecke, D., D. Makowski, M. S. Ben-Shachar, I. Patil, and P. Waggoner. 2020. *performance*: Assessment of regression models performance. (Available from: https://easystats.github.io/performance/)

Matter, S. F. 2000. The importance of the relationship between population density and habitat area. Oikos 89:613–619.

Mitchell, F. L., and J. L. Lasswell. 2018. Population characteristics of the dragonfly *Pantala flavescens* colonizing small constructed ponds. Southwestern Entomologist 43:833–839.

Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of the Royal Society: Interface 14(134).

Ortega, J. A., M. Gómez-Heras, R. Perez-López, and E. Wohl. 2014. Multiscale structural and lithologic controls in the

development of stream potholes on granite bedrock rivers. Geomorphology 204:588–598.

Pebesma, E. 2018. Simple features for R: Standardized support for spatial vector data. The R Journal 10:439–446.

Peckarsky, B. L., P. R. Fraissinet, M. A. Penton, and D. J. Conklin Jr. 1993. Freshwater macroinvertebrates of northeastern North America. Cornell University Press, Ithaca, New York.

Pelletier, J. D., K. E. Sweeney, J. J. Roering, and N. J. Finnegan. 2015. Controls on the geometry of potholes in bedrock channels. Geophysical Research Letters 42:797–803.

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences 105:20,770–20,775.

Ren, H., X. Yuan, J. Yue, X. Wang, and H. Liu. 2016. Potholes of mountain river as biodiversity spots: Structure and dynamics of the benthic invertebrate community. Polish Journal of Ecology 64:70–83.

Robinson, C. T., K. Tockner, and J. V. Ward. 2002. The fauna of dynamic riverine landscapes. Freshwater Biology 47:661–677.

Schenk, K., F. Suhling, and A. Martens. 2004. Egg distribution, mate-guarding intensity and offspring characteristics in dragonflies (Odonata). Animal Behaviour 68:599–606.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients: Interpretation of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Schuler, M. S., J. M. Chase, and T. M. Knight. 2017. Habitat patch size alters the importance of dispersal for species diversity in an experimental freshwater community. Ecology and Evolution 7:5774–5783.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: The colonization of empty islands. Ecology 50:278–296.

Solt, F., Y. Hu, O. Keyes, B. Bolker, S. Müller, T. Leeper, C. Wallace, and C. Warshaw. 2018. *dotwhisker*: Dot-and-whisker plots of regression results. (Available from: http://CRAN.R-project.org /package=dotwhisker)

Steffan-Dewenter, I., and T. Tscharntke. 2000. Butterfly community structure in fragmented habitats. Ecology Letters 3:449–456.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Tennessen, K. J. 2019. Dragonfly nymphs of North America: An identification guide. Springer Nature, Cham, Switzerland.

Thompson, P. L., B. Rayfield, and A. Gonzalez. 2017. Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. Ecography 40:98–108.

Tockner, K., F. Malard, and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes 14:2861–2883.

Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer, and J. V. Ward. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). Freshwater Biology 41:521–535.

Van Buskirk, J. 1989. Density-dependent cannibalism in larval dragonflies. Ecology 70:1442–1449.

Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8:2–8.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.

Wickham, H., W. Chang, L. Henry, T. L. Pedersen, K. Takahashi, C. Wilke, K. Woo, H. Yutani, and D. Dunnington. 2016. *ggplot2*: Elegant graphics for data analysis. (Available from: https://ggplot2 .tidyverse.org)

With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76:2446–2459.

Wright, A. H., and A. A. Wright. 1949. Handbook of frogs and toads of the United States and Canada. Comstock Publishing Associates, Ithaca, New York, New York.

Zuur, A. F., and E. N. Ieno. 2016. A protocol for conducting and presenting results of regression-type analyses. Methods in Ecology and Evolution 7:636–645.