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Article

Diversity Patterns Associated with Varying Dispersal Capabilities as a Function of Spatial and Local Environmental Variables in Small Wetlands in Forested Ecosystems

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Received: 21 September 2020; Accepted: 27 October 2020; Published: 29 October 2020



Abstract: The diversity of species on a landscape is a function of the relative contribution of diversity at local sites and species turnover between sites. Diversity partitioning refers to the relative contributions of alpha (local) and beta (species turnover) diversity to gamma (regional/landscape) diversity and can be influenced by the relationship between dispersal capability as well as spatial and local environmental variables. Ecological theory predicts that variation in the distribution of organisms that are strong dispersers will be less influenced by spatial properties such as topography and connectivity of a region and more associated with the local environment. In contrast, the distribution of organisms with limited dispersal capabilities is often dictated by their limited dispersal capabilities. Small and ephemeral wetlands are centers of biodiversity in forested ecosystems. We sampled 41 small and ephemeral wetlands in forested ecosystems six times over a two-year period to determine if three different taxonomic groups differ in patterns of biodiversity on the landscape and/or demonstrate contrasting relationships with local environmental and spatial variables. We focused on aquatic macroinvertebrates (aerial active dispersers consisting predominantly of the class Insecta), amphibians (terrestrial active dispersers), and zooplankton (passive dispersers). We hypothesized that increasing active dispersal capabilities would lead to decreased beta diversity and more influence of local environmental variables on community structure with less influence of spatial variables. Our results revealed that amphibians had very high beta diversity and low alpha diversity when compared to the other two groups. Additionally, aquatic macroinvertebrate community variation was best explained by local environmental variables, whereas amphibian community variation was best explained by spatial variables. Zooplankton did not display any significant relationships to the spatial or local environmental variables that we measured. Our results suggest that amphibians may be particularly vulnerable to losses of wetland habitat in forested ecosystems as they have high beta diversity. Consequently, the loss of individual small wetlands potentially results in local extirpations of amphibian species in forested ecosystems.

Keywords: amphibian; dispersal; beta diversity; ephemeral wetland; zooplankton; macroinvertebrate; variation partitioning; forested wetland

1. Introduction

Understanding drivers and consequences of changes to biodiversity is an important goal of ecologists due to the effects that it has on the earth's ecosystems as well as to better inform conservation methods as the Earth undergoes its sixth major extinction event [1]. Freshwater forested ecosystems are one of the most threatened ecosystems due to clearing, dams, channelization, and sea level rise, and they harbor a large share of biodiversity [2–4]. Forested wetland habitats have unique features that have strongly affected the traits of the species that rely on them for much if not all of their history [5–7].

Characterizing biodiversity patterns can give insight into how biodiversity can be maintained and protected in a world that is increasingly altered via anthropogenic activities [8]. The diversity of species in a landscape can be divided between alpha (local) diversity, e.g., the average species richness of sites in a landscape and beta diversity, i.e., the turnover of species between sites. Gamma diversity describes the overall diversity in the region and is a combination of alpha and beta diversity. Equivalent regional diversities can be obtained via high species richness at local sites and low turnover between sites or by having low richness at individual sites and high turnover. Differences in dispersal ability between taxonomic groups can lead to differences in how diversity is partitioned throughout a landscape and the relative importance of local environmental factors and species interactions in structuring species assemblages [9,10]. For example, high rates of dispersal have been predicted to reduce beta diversity [11].

Small and ephemeral wetlands are centers of biodiversity in forested ecosystems [12–14]. Ephemeral wetlands are characterized by regular drying stages that strongly influence community structure and biodiversity [15]. The biodiversity of ephemeral and other small wetlands could be controlled by either local or regional factors, or a dynamic balance between local and regional factors over time. Local factors are those that affect diversity at small scales such as the local environmental conditions or species interactions, and regional factors affect diversity via larger scale processes [16]. Examples of regional processes include dispersal, speciation, and widespread environmental changes such as drought [17]. It is also possible that the dispersal capabilities of various taxa, (e.g., zooplankton, aquatic macroinvertebrates, and amphibians) could interact with local and regional forces such that dispersal capability could determine the relative influence of local and regional factors for different taxonomic groups [18]. For example, organisms with limited dispersal capabilities, such as slow crawling (e.g., salamanders) or hopping (e.g., frogs), would tend to show community patterns associated with spatial patterns of critical habitats (e.g., ephemeral wetlands) on the landscape [19]. Colonization, recolonization, and dispersal are thought to be important processes in ephemeral aquatic habitats due to regular local extirpations of functional communities as a result of periodic drying or other sources of stochasticity [20,21]. Subsequently, animals that use ephemeral wetlands must either have a life history stage that does not require standing water or must be capable of moving to a different area [22]. Ephemeral wetlands are home to species such as zooplankton and aquatic macroinvertebrates that are capable of either active or passive aerial dispersal as a result of a drying event [23–25]. Many species of amphibian depend on ephemeral wetlands for breeding and early development, and typically there is a significant post-metamorphosis dispersal event by juveniles coinciding with wetland drying [26]. Developing amphibians have adaptations related to drying rates and wetland emergence [27]. Post-breeding adults generally leave ephemeral wetlands and shift macrohabitats to areas that are physiologically conducive until the next filling cycle occurs, which is timed with seasonal breeding activity [28]. The result of the continuous cycle of drying, re-wetting, and drying is that community assembly occurs at more frequent intervals in ephemeral wetlands.

In practice, biodiversity is often examined in smaller, more tractable units by grouping subsets of the community using variables such as taxonomic relatedness, size, habitat type, or other variables. In this study we describe biodiversity patterns of three different taxonomic groups with different dispersal methods that are found in small and ephemeral wetlands within forested ecosystems in the Piedmont and Blue Ridge regions of South Carolina, USA. We were interested in the potential for different taxonomic groups (zooplankton, amphibians, and macroinvertebrates) to display varying

diversity patterns regarding spatial and local environmental variables. Adult amphibians have been documented having a range of dispersal distances including up to 1.6 km although most are in the range of 159–290 m [29]. Another study by [30] found dispersal distances of 105–866 m for three species of newt and 170–2214 m for four species of frog. For this study, amphibians will be considered weak active dispersers.

In a similar vein, taxonomic groups such as adult aquatic macroinvertebrates, largely consisting of flying insects (in our study, 73% of the presence/absence data consisted of the class Insecta), are capable of strong directed dispersal. Organisms that are capable of directed flight could potentially evaluate multiple sites for colonization, and would therefore show community patterns that are less affected by distance between ephemeral wetlands but would be affected by local environmental variables [19]. Zooplankton are considered passive dispersers and are thought to be primarily wind dispersed or dispersed via phoresy, possibly on the feet or feathers of aquatic birds [13,25,31]. Different dispersal abilities are hypothesized to result in varying diversity outcomes in ephemeral wetlands for different taxonomic groups.

We hypothesized that increasing active dispersal capabilities would lead to decreased beta diversity, increased alpha diversity, and more influence of local environmental variables on community structure with less influence of spatial variables. We predicted that zooplankton would have high beta diversity that was primarily driven by spatial variables, amphibians would have high beta diversity that was primarily driven by spatial variables, and that macroinvertebrates (primarily insects) would have lower beta diversity and high amount of community structure would be associated with local environmental variables. Additionally, we offer insights regarding the relative importance of local and regional drivers of diversity for each of the respective taxonomic groups and how the relative importance of local and regional drivers can be used to inform management decisions.

2. Methods

2.1. Study Area

The southern Appalachian region of the southeastern United States is globally significant for the exceptionally high biodiversity it supports, especially for amphibians, freshwater species, and temperate broadleaf and mixed forest species [32]. The diverse topography, warm, rainy climate, and lack of past glaciation contributes to the high biodiversity found in the southern Appalachian region [33]. The topography within the southern Appalachian region spans from steep mountainous terrain in the Blue Ridge ecoregion to rolling foothills in the Piedmont ecoregion [34]. Temperate broadleaf and mixed forests typify the landscape, yet the area is undergoing rapid urbanization and land use change [34]. Surface waters within the region include lotic systems (e.g., headwater streams, tributaries, rivers), impoundments, and wetlands inclusive of small, ephemeral wetlands that are essential for supporting biodiversity within the forested landscape [35]. Land use and land cover change (e.g., deforestation, urbanization), climate change, and other anthropogenic stressors threaten these terrestrial and aquatic ecosystems and biodiversity within this region, much as they do elsewhere [33,36–38].

As part of a larger study to improve knowledge about wetlands in an area undergoing rapid land use change, Pitt et al. [35] used remote sensing and local ecological knowledge to map 10506 small, ephemeral, and/or isolated wetlands in forests within the Piedmont and Blue Ridge ecoregions of South Carolina. Of these wetlands, 4611 were not mapped by the NWI (National Wetlands Inventory), likely due to the small size of the wetlands and coarse resolution of the available remote sensing data, and thus would likely be excluded from regulatory protections and land management and conservation planning [35]. We selected 41 of the newly mapped (i.e., non-NWI) small and ephemeral wetlands for intensive field-based study over a two-year period (Figure 1). We collected abiotic and biotic data from each of the 41 target wetlands over a minimum of 3 site visits per year (i.e., ≥ 6 site visits total) between January and June and once in November. Site visits were timed to maximize detectability based

on amphibian breeding phenology. Similarly, the two-year time period was intended to maximize detectability of species that may exhibit inter-annual variability in their activity or abundance.

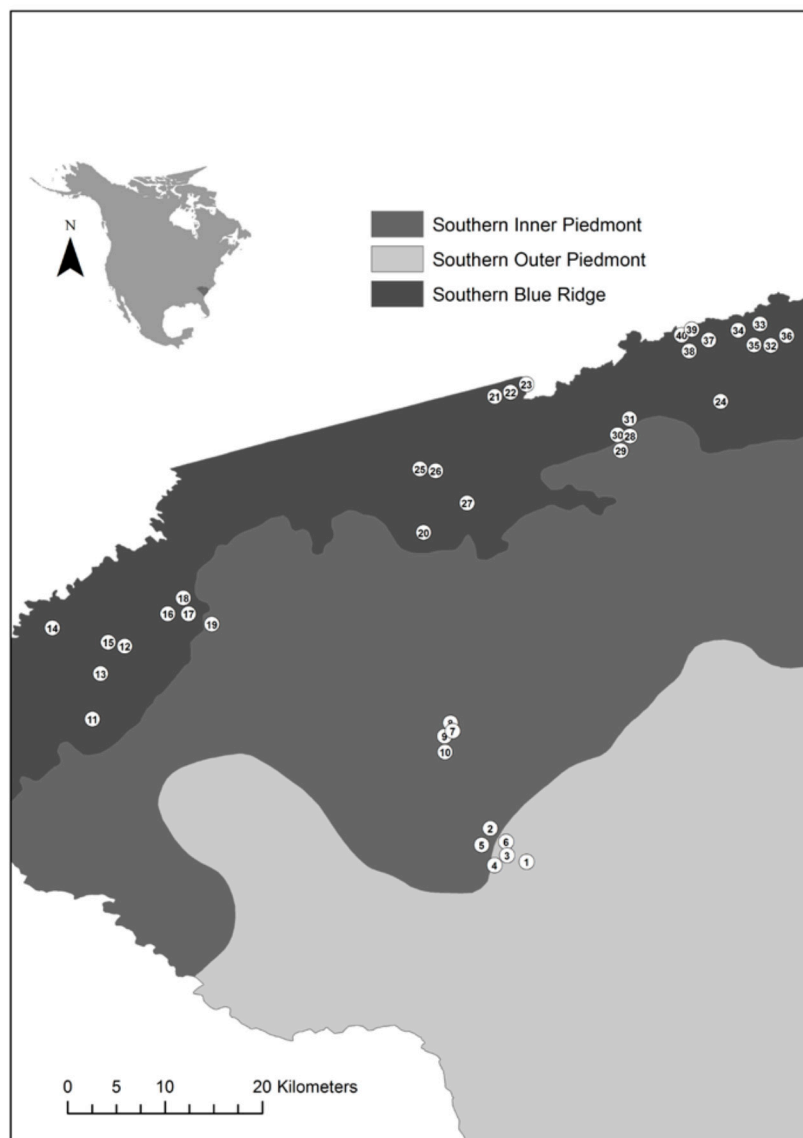


Figure 1. Map of the study sites.

2.2. Environmental Predictors

2.2.1. Wetland Metrics

We visually searched the perimeter of each wetland for evidence of temporary or permanent inlets, outlets, and/or connections with other water bodies. Distance from each wetland to the nearest delineated stream centerline was calculated using the “measure” tool in ArcGIS 10.1. We determined length and width of each wetland based on the surface water in cases where no evidence of drying had occurred (i.e., the permanent footprint of the wetland was filled with water) or based on the permanent footprint of the wetland if substantial drying had occurred using an open reel measuring tape (Keson Industries, Aurora, IL, USA). These measurements were used to calculate an approximation of maximum wetland area. We measured the maximum depth of each wetland at its deepest point using a metal measuring tape (Stanley Tools Product Group, New Britain, CT, USA). The deepest point of each wetland was determined by visually assessing each wetland to determine the general area(s) with the greatest depth (i.e., the deepest point), then we measured between 5 and 10 points in the

targeted area(s) of the wetland, depending on the wetland size and depth variability, and recorded the maximum depth measured. We also identified areas that appeared to have the most representative water depth for each wetland. We measured the depth at 5–10 points in the targeted area(s) of the wetland and recorded mean representative depth. Hydrological status (e.g., standing water, dry) of each wetland was noted during each site visit and used to categorize wetlands as either ephemeral or permanent.

We estimated percent canopy cover over and around the perimeter of the wetland using a GRS vertical tube densitometer (Geographic Resource Solutions, Arcata, CA, USA; [39,40]) because canopy cover can influence a variety of local environmental parameters including water temperature, dissolved oxygen, and light availability, and by extension, wetland drying/evaporation rates, developmental rates of ectothermic organisms, food resource availability, and nutrient dynamics [41–43]. Over-wetland canopy cover was estimated based on the percentage of data points containing canopy along a transect that bisected the longest axis of the pool. Perimeter canopy cover was estimated based on the percentage of data points containing canopy along a perimeter ring located 5 m from the edge of the wetland. Canopy cover data were collected every 3 m along the bisecting transect and perimeter ring surrounding the wetland, when possible, based on wetland size. When wetland size prohibited the collection of an adequate number of data points based on the 3 m collection criteria, over-wetland canopy cover data were collected at a minimum of four points along the bisecting transect.

2.2.2. Water Quality

Water pH, temperature, conductivity, turbidity, dissolved oxygen (DO), and oxidative reductive potential (ORP) were measured using a YSI 6-series Multiparameter Water Quality Sonde (model 6600 V2-4) outfitted with relevant probes and outputting to a Multiparameter Display System (model YSI 650 MDS; YSI Inc., Yellow Springs, OH, USA). In year 1, we analyzed total nitrogen (TN), total phosphorus (TP), and coliform bacteria content for each wetland. We collected water samples from centrally located areas within the wetlands using autoclave sterilized, acid-washed bottles and, when necessary, a swing sampler. Total coliform bacteria and *Escherichia coli* content, which are known to be variable in wetlands based on both anthropological and wildlife inputs [44], were quantified using the Colilert Test Kit and Quanti-Tray/2000 (IDEXX Laboratories, Inc., Westbrook, ME, USA) method.

2.2.3. Phytoplankton and Benthic Algae Biomass

Biomass estimates of phytoplankton and benthic algae are useful indicators for assessing ecological condition of wetlands, as phytoplankton and benthic algae serve as food resources, contribute to nutrient and energy cycling, can provide desiccation-resistant habitat, and are sensitive to changes in water quality [45]. Using grab samples or a swing sampler (Nasco, Fort Atkinson, WI, USA), we collected water samples from centrally located areas within the wetlands for phytoplankton biomass analysis. We collected benthic algae samples by placing the sample bottle mouth straight down onto the bottom of the wetland. By placing the sample bottle mouth straight down into the wetland we could create an air pocket in the bottle which allowed us to not sample from the water column. While securely holding the bottle mouth down with one hand, the sampler slid her other hand under the bottle's mouth and secured the loose debris and water in the bottle with the palm of the hand. The sampler would then quickly flip the bottle without losing its contents and secure the bottle cap. This method is consistent with standard methods for assessing benthic algae in areas of freshwater ecosystems with soft or loose substrate [46,47]. Phytoplankton and benthic algae samples were collected and transported in amber Nalgene bottles (ThermoFisher Scientific Inc., Waltham, MA, USA) as we intended on quantifying biomass based on chlorophyll *a* content. In the laboratory, each sample was thoroughly mixed by 30 seconds of shaking. We measured sample volume using a graduated cylinder. We filtered samples using a vacuum filtration apparatus fitted with a Whatman grade GF/C glass microfibre filter (Whatman plc, Kent, UK). We rinsed the graduated cylinder into the filtration cup and the sides of filtration cup using distilled water to ensure that the entire (sub)sample was filtered.

Following water extraction, we folded the filters in half to protect the sample and placed each sample into an individual, labeled Whirl-Pak bag (Nasco, Fort Atkinson, WI, USA). Samples were frozen until analysis. Phytoplankton and benthic algae biomass were determined using the chlorophyll *a* biomass analysis described by [48].

2.3. Response Variables

2.3.1. Amphibians

In addition to timing sampling events with amphibian breeding phenology, we employed multiple survey techniques to further maximize detection of amphibians and establish species use. Prior to other sampling, we approached wetlands in silence and listened for amphibian calls for 5–10 min, depending on the variety of species heard. Following call surveys, we visually surveyed the water and banks of the wetland for amphibian adults, eggs, and larvae. We searched for amphibians under rocks, logs, and other objects within 5 m of the wetland, being careful to return features to their original locations and positions to maintain the integrity of the wetlands and surrounding habitats. We used dip nets to survey larval amphibians, in addition to examining larval amphibians captured during macroinvertebrate sampling (see next section). Field-identified amphibians were released at their location of capture. We collected voucher specimens of larval amphibians that were not easily identified in the field. Voucher specimens were anesthetized and dispatched using a 1:12,500 neutral buffered Finquel MS-222 (Argent Chemical Laboratories Inc., Redmond, WA, USA) solution, then preserved in a neutral buffered 10% Formalin solution and stored in glass collection jars. Voucher specimens were identified using a dissecting microscope.

2.3.2. Aquatic Macroinvertebrates

We collected aquatic macroinvertebrate samples using a D-frame dip net (500 μ m mesh size; Wildlife Supply Company, Yulee, FL, USA). We placed a 30.5 \times 30.5 cm sampling frame in a representative area of each wetland to delineate the sampling area. We then physically disturbed the substrate within the sampling frame into the D-frame dip net. Within the net, with the net still partially submerged, we tousled the leaves vigorously to detach the invertebrates from the leaves. Leaves and amphibian larvae were carefully removed from the net and leaves were inspected to ensure that all macroinvertebrates were removed. Samples were preserved in 70% ethanol and stored in Whirl-Pak bags (Nasco, Fort Atkinson, WI, USA). All aquatic macroinvertebrates from each sample were identified to the lowest possible level, usually genus, using a dissecting microscope.

2.3.3. Zooplankton

We used a Wisconsin sampler (80 μ m mesh size; Wildlife Supply Company, Yulee, FL, USA) to sample zooplankton. Shallow water depth precluded the use of the standardized method for sampling zooplankton where the Wisconsin sampler is drawn up from the bottom of the water body (or some other known water depth) as described by Ward and Whipple [49]. Thus, we collected approximately 1.5 L of water from the wetland using a Nalgene sampling bottle (ThermoFisher Scientific Inc., Waltham, MA, USA) and poured the sample through the Wisconsin sampler. Samples were preserved in 70% ethanol and stored in Nalgene bottles (ThermoFisher Scientific Inc., Waltham, MA, USA). All zooplankton from each sample were identified to the lowest possible level, generally Order (copepods) or family (Cladocerans) using a combination of a dissecting microscope and a compound microscope.

2.3.4. Statistical Analyses

We performed diversity partitioning, community distance decay relationships, and variation partitioning to determine if differing dispersal capabilities would be associated with different diversity patterns for each taxonomic group. All analyses were performed using the R programming language [50].

Due to differences in detectability among the three taxonomic groups, all analyses were conducted with presence/absence data or the functional equivalent.

We used the “d” function in the vegetarian R 3.4.0 package [51] to partition biodiversity of macroinvertebrates, amphibians, and zooplankton into alpha, beta, and gamma diversity with the order of the diversity measure q , set to 0. Setting $q = 0$ results in no weighting of species abundances on the diversity value, consequently resulting in values that can be interpreted as species richness. Partitioning diversity into alpha, beta, and gamma diversity enables local species diversity (alpha) to be compared to species turnover (beta) with regards to regional diversity (gamma) of a given taxonomic group. Partitioning diversity enables comparisons of how much each type of diversity contributes to overall biodiversity. For example, high regional diversity could be due to high species turnover between sites or high local diversity at individual sites. Since macroinvertebrates and zooplankton samples were only taken in the first year of sampling, we restricted diversity partitioning to the first year for amphibians despite having two years of data. The “d” function in the vegetarian R package implements the methods described in [52,53], which allows for independent alpha and beta diversities. We also calculated standard errors for the diversity partitioning using the “bootstrap” function in the vegetarian package [54].

We used variation partitioning to explore the contributions of spatial and local environmental variables to community composition of zooplankton, macroinvertebrates, and amphibians in ephemeral wetlands [55]. Variation partitioning is a multivariate technique that allows the variation in one response matrix to be explained by multiple other predictor matrices. The variation explained by each predictor matrix is calculated as if the second matrix is a co-variate and with the effects of the second matrix partialled out of the response matrix. Then the process is repeated with the order of predictor matrices switched.

To obtain the necessary statistical power and reduce the number of zeroes in the dataset, particularly for amphibians, samples from each taxonomic group in each wetland were aggregated through time. We also calculated the mean for each local environmental variable for all visits combined for each site. Spatial variables were obviously the same for all visits as the ponds did not change location. The response matrix was a site X species matrix of either zooplankton, macroinvertebrates, or amphibians. Extremely rare species or taxonomic groups with only a single instance of occurrence were excluded from the analysis because they contribute unexplainable variance [56]. We did not perform occupancy modeling for each species due to the complexity of such an analysis. However, we did transform the species abundance matrices to presence/absence data to minimize the effects of differences in detectability of the different species on the results. The spatial matrix consisted of 2-dimensional Euclidean distances transformed by the Principal Coordinates of Neighborhood Matrix (pcnm R function in the Vegan package) [57]. The local environmental predictor matrix contained standardized local environmental variables on a scale of 0–1 to minimize the effects of varying scales on the results. We visually checked for collinearity of local environmental variables and removed those that were collinear with one or more other variables. We retained the local environmental variables of nitrate concentration, elevation, water temperature, water conductivity, water turbidity, dissolved oxygen, ORP, *E. coli* content, mean representative pool depth, pool area, and benthic algae.

We used the varpart R function in the Vegan R package to perform the variation partitioning [58]. The ‘rda’ function in the Vegan R package was used to test the significance of the overall models and the variation partitioning model terms by calculating the same model parameters as in the variation partitioning and then using the function anova.cca (Vegan R package) to perform permutation tests to ascertain the significance of the model terms.

3. Results

Macroinvertebrates, zooplankton, and amphibians varied in how diversity was partitioned between local assemblage diversity (alpha) and species turnover (beta) among patches (Figure 2).

Alpha and beta diversity were similar for macroinvertebrates, indicating both types of diversity made similar contributions to overall gamma diversity. Zooplankton beta diversity was low, with alpha diversity being the primary contributor to gamma diversity. Amphibian alpha diversity was low compared to beta diversity, indicating that species turnover among ephemeral wetlands was the greater driver of adult amphibian diversity (Figure 2).

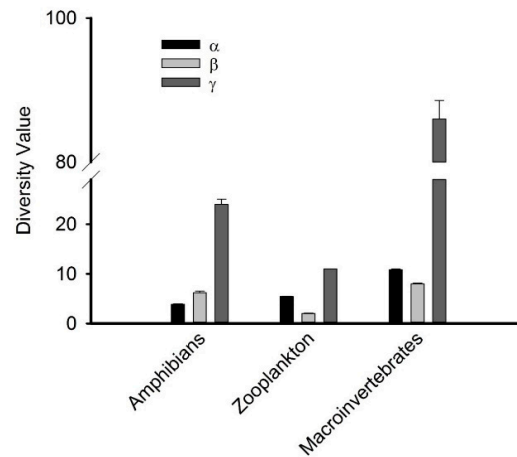


Figure 2. Diversity partitioning for amphibians, zooplankton, and macroinvertebrates. Alpha diversity is the average diversity of a single ephemeral wetland, beta diversity is the number of species turnover between wetlands, and gamma diversity the total amount of diversity present in the study for a taxonomic group. Gamma diversity is mathematically related to beta and alpha diversity $\gamma = \alpha \times \beta$. Error bars are \pm SE.

Variation partitioning results showed that taxonomic groups with varied dispersal capabilities differ in the amount of community variation explained by spatial and local environmental variables (Figure 3). All models were significant or marginally significant ($p < 0.06$) except for zooplankton (Table 1). Variation in macroinvertebrate communities was significantly associated with local environmental variables. Amphibian community patterns were significantly associated with spatial variables. Zooplankton community variation was not significantly related to the local environmental variables or spatial variables.

Table 1. *p*-values and pseudo F-statistics for RDA models for each taxonomic group and RDA model terms. Values were obtained via Monte-Carlo simulations. Bolded *p*-values are significant at $\alpha \sim 0.05$ level.

Taxa	Variables	Adj R ²	F	<i>p</i> Value
Amphibians		0.15	1.304	0.047
	Space (a + b)	0.11	1.53	0.012
	Environment (b + c)	0.03	1.26	0.093
	Environment Space (a)	0.03	1.36	0.308
	Space Environment (b)	0.12	1.09	0.057 *
Zooplankton		0.05	1.06	0.41
	Space (a + b)	0.00	0.95	0.573
	Environment (b + c)	0.00	1.08	0.37
	Environment Space (a)	0.05	1.13	0.31
	Space Environment (b)	0.10	1.05	0.38
Macroinvertebrates		0.144	1.22	0.058 *
	Space (a + b)	0.02	1.00	0.50
	Environment (b + c)	0.14	1.26	0.056 *
	Environment Space (a)	0.12	1.58	0.003
	Space Environment (b)	0.00	1.19	0.09

RDA—please define. * please define.

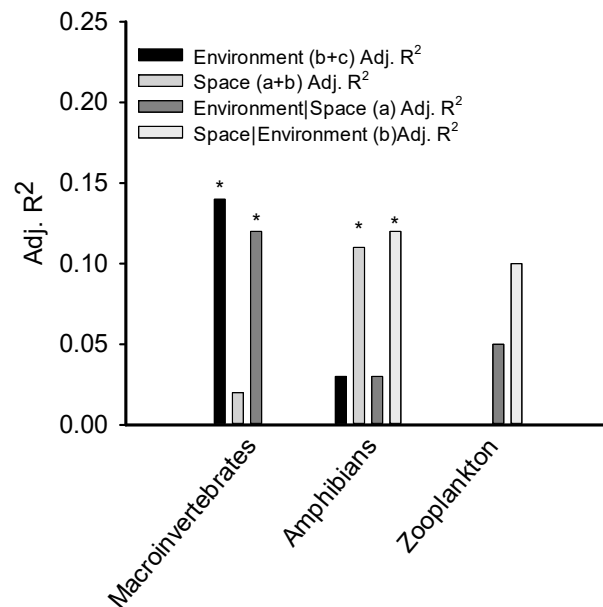


Figure 3. Bar plot showing the amount of community variation explained by spatial and local environmental variables. Local environment is variation explained by the local environment matrix with the spatial matrix as a covariate. Space is the variation explained by the spatial matrix with the local environment matrix as a covariate. Environment|Space is the variation explained by environment independent of the spatial matrix. Space|Environment is the variation explained by the spatial matrix independent of the environmental matrix. * denotes significance of each effect at $\alpha \sim 0.05$.

4. Discussion

We found that zooplankton, amphibians, and macroinvertebrates displayed contrasting patterns with regards to diversity partitioning and the amount of community variation explained by spatial and local environmental variables. The differences in community variation between these taxonomic groups offer insight into how spatial and local environmental variables affect community composition as well as implications for conservation of organisms that inhabit ephemeral wetlands located within a forested matrix.

Amphibians, while capable of active dispersal, may not venture more than a few hundred meters from their natal spawning wetlands [59]. Pool-breeding amphibians generally disperse as juveniles and overcome physiological and morphological barriers to long distance movement by staging dispersal over several years [28]. Philopatry is common in pool-breeding amphibians, reducing use of distant pools in favor of return to productive breeding sites [28,60]. Despite the difficulty of studying amphibian dispersal, two multi-year, landscape level programs delivered estimates that between 9% and 18.5% of juveniles disperse to new wetlands [61]. Successful long distance emigration results in impressive genetic distances recorded for productive breeding sites that are more than 1 km apart [62]. Metacommunity dynamics on relatively short time scales are likely less influenced by these rare dispersal events [63]. Our results agree with these findings as the amphibian communities in our study appear to be dispersal limited, which can explain the high levels of beta diversity for amphibian communities and the relatively larger proportion of community variance explained by spatial variables. Removing the effects of environment slightly increased the amount of variation space could explain, suggesting that with respect to amphibians, local environmental and spatial variables were correlated in the sense that sites that were closer together were more similar in their local environmental variables. Our finding is in agreement with other studies that have shown strong effects of both local environmental factors and spatial variables on amphibian communities, although in our case, environment on its own did not significantly explain amphibian community variation [64,65] but see [66].

Amphibian regional diversity in our study was primarily driven by beta diversity. The average ephemeral wetland only contained 3.9 species of amphibian but there was a total of 24 species detected. If amphibian alpha diversity is low within wetlands but beta diversity is high, the loss of individual ephemeral wetlands could have unusually detrimental effects on regional amphibian diversity. High fidelity to natal sites is common for amphibians utilizing ephemeral wetlands for breeding [59,61]. Alternatively, when faced with the loss of one ephemeral wetland, amphibian species may simply use another similar, nearby wetland for reproduction [67]. Evidence exists that adult amphibians can select egg deposition sites and distinguish suitable ephemeral wetlands from unsuitable wetlands [68].

Zooplankton are capable of passive dispersal and are not capable of selecting their habitats on the scale of individual ephemeral wetlands [31]. Zooplankton gamma diversity was driven primarily by alpha diversity. Zooplankton community variation was not associated with spatial variables or local environmental variables. Previous studies have detected possible spatial and environmentally driven patterns for zooplankton communities [69,70]. However, the lack of significant effects of environment and spatial variables in our study may be the result of relatively coarse identification levels. Macroinvertebrates were generally identified to genus and amphibians were identified to species whereas zooplankton were usually identified to order (copepods) or family (Cladocerans). We used presence/absence data in all our analyses and most our samples contained Harpacticoid, Cyclopoid, and Calanoid copepods as well as Daphniidae, Culicidae, and Collembola. With less variation between samples, there was less variation to be partitioned between spatial and local environmental variables leading to a lack of significant differences when testing significance using permutation tests.

Macroinvertebrate adults are often capable of active dispersal as a result of either directed overland travel or aerial flight [71]. They are able to infer habitat suitability using a variety of sensory cues, in some cases before actually colonizing the habitat [72,73]. In our survey, macroinvertebrate community variation was explained primarily by local environmental variables and gamma diversity was driven by relatively even contributions of alpha and beta diversity. Consequently, our results support the conclusion that macroinvertebrate communities in ephemeral wetlands are heavily influenced by local environmental conditions.

Variation in the communities of active aerial dispersers such as macroinvertebrates was affected by local environmental variables whereas zooplankton (passive dispersers) and amphibians (active terrestrial dispersers) were not. Amphibian diversity in the ephemeral wetlands in our study was strongly driven by species turnover among sites (beta diversity) whereas macroinvertebrates had more even contributions of beta diversity and alpha diversity to overall regional diversity (gamma diversity). Others studies have observed that regional amphibian diversity is strongly driven by beta diversity [74]. Some researchers suggest that amphibian turnover is driven by opportunistic species, capitalizing on changing local conditions in wetlands to maximize reproductive potential [75].

Amphibians, active but limited to overland dispersal, had comparatively high beta diversity values. The negative correlation between beta diversity and dispersal capabilities is predicted via simulation modeling although as we saw in this study, it may not hold in every taxonomic group [11]. Evidence from research utilizing natural systems also indicates that, for taxonomic groups differing in dispersal capabilities but occupying similar habitats, increased dispersal capabilities correlate with decreased beta diversity [9,76] but see [77]. Essentially, high levels of dispersal act to homogenize local communities and consequently allow for better competitors to dominate less competitive species. At lower levels of dispersal for a taxonomic group, better competitors do not make it to all habitat patches allowing for less competitive species to coexist on a metacommunity scale. Understanding the relationship between dispersal capability or rate and community processes is vital to understanding how communities are assembled and maintained [78]. However, for our study, it is difficult to determine if high beta diversity for amphibians was a result of site fidelity, e.g., amphibians tending not to disperse to new breeding ponds, or actual dispersal limitation.

Dispersal and migration capabilities have long been a topic of concern for management of ephemeral wetlands yet little attention has been given to simultaneous consideration of multiple taxonomic groups [79,80]. Our study justifies concerns that amphibian declines may be exacerbated by increased habitat fragmentation from a metacommunity and metapopulation perspective and that dispersal limitation may be a driver of amphibian declines [81]. It also suggests that using one taxonomic group, e.g., macroinvertebrates, as an indicator of site quality may be an inadequate approach. When the communities of zooplankton, macroinvertebrates, and amphibians are considered, it becomes clear that the relative dispersal limitations of amphibians make them a more sensitive indicator of landscape-level fragmentation than either of the other groups.

The utility and importance of wetlands as biodiversity hotspots and providers of ecosystem services has been recognized for the last 40–50 years [82–84]. However, the importance of individual smaller wetlands in a regional management or conservation context has generally been given less attention [85,86]. By ensuring the preservation of distinct wetlands, some of which are ephemeral, the loss of the denizens of any single wetland can be recovered via recolonization of that wetland from adjacent wetlands. However, ephemeral ponds are not afforded the same protections as more permanent bodies of water and often not even delineated on maps [35].

The current iteration of the Clean Water Act specifies that ephemeral features, inclusive of ephemeral wetlands, are not considered “waters of the United States, and are thus excluded from federal regulatory protection [87]. Our results suggest a holistic or regional-based approach to wetland and forest conservation in which the needs of multiple taxonomic groups are simultaneously examined to ensure the maximum amount of native biodiversity, and by extension ecosystem function, is conserved. We suggest increased protections for ephemeral wetlands with specific emphasis on ensuring dispersal corridors remain intact would be an effective strategy to reduce the loss of biodiversity. Dispersal serves to restore local communities that have been negatively affected by mortality events and demographic stochasticity but for dispersal to have an effect, there must be intact communities within dispersal range to disperse to/from.

In conclusion, we demonstrated that dispersal capability of taxonomic groups is associated with how diversity is partitioned between alpha, beta, and gamma diversity, as well as how community variation is explained by the local environment and spatial relationships between local sites. Forested landscapes house small and ephemeral wetlands that are home to a variety of organisms whose dispersal, births, and deaths are potentially affected very differently with regards to the effects of spatial and local environmental variables. As such, forest and landscape level management and planning techniques need to account for these differences.

Author Contributions: Conceptualization, B.M.T., A.L.P., B.L.B., R.F.B.; Methodology, B.M.T., A.L.P., B.L.B., R.F.B., and J.H.-H.; Formal Analysis B.M.T.; Resources, B.L.B., R.F.B.; Writing—Original Draft Preparation, B.M.T., A.L.P.; Writing—Review & Editing, B.M.T., A.L.P., B.L.B., R.F.B., J.H.-H.; Visualization, B.M.T.; Supervision, A.L.P., R.F.B., B.L.B.; Project Administration, A.L.P., R.F.B., B.L.B.; Funding Acquisition, B.L.B., R.F.B. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by a U.S. EPA Region 4 Wetland Program Development Grant.

Acknowledgments: Research was approved by Clemson University’s Institutional Animal Care and Use Committee. Research was implemented under permits from the South Carolina Department of Natural Resources, South Carolina State Park System, and U.S. Department of Agriculture—Forest Service. We thank the South Carolina State Park, South Carolina Department of Natural Resources, U.S. Forest Service, Clemson Experimental Forest, and Upstate Forever personnel, Margaret H. Lloyd Endowment, Technical Contribution No. 6917 of the Clemson University Experiment Station, as well as J. Garten, for assistance in locating wetlands and monitoring amphibian activity. We thank the numerous Clemson University students who participated in field and lab work for this project, and J. Pike for analyzing macroinvertebrate samples.

Conflicts of Interest: The authors declare no conflict of interest.

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