Wetlands (2022) 42:75
https://doi.org/10.1007/s13157-022-01596-w

COASTAL WETLANDS

Patterns of Invertebrate Community Composition and Functional Structure Across a Dune Succession Gradient

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Received: 29 October 2021 / Accepted: 29 August 2022 / Published online: 16 September 2022

Abstract

The world's most extensive freshwater sand dunes lie along the eastern shore of Lake Michigan, USA. These dunes follow a succession gradient from open canopy, grass-covered dunes to forested dunes further inland with wetlands interspersed in the dune landscape. We asked if macroinvertebrate assemblages in interdunal wetlands showed predictable change along the dune succession gradient. In April through October 2017, we collected physical–chemical data, characterized wetland habitat, and macroinvertebrate assemblages at 11 interdunal wetlands distributed along an open-forested dune gradient. We evaluated patterns of taxonomic diversity and abundance and functional richness, community composition, and community dissimilarity along the gradient. The dune gradient represented changes in water chemistry variables associated with terrestrial and aquatic vegetation. Overall, interdunal wetlands in open dune habitat showed lower taxonomic diversity and were dominated by communities with functional traits tailored to variable habitats (active dispersal, bi/multi-voltine). Variation in assemblage composition along the gradient is correlated with differences in water temperature, pH, dissolved oxygen, and amount of surrounding terrestrial vegetation. Community dissimilarity is driven primarily by terrestrial vegetation surrounding wetlands and secondarily by spatial location. This is the first study to document aquatic diversity across a dune succession gradient illustrating that terrestrial dune vegetation has a large impact on patterns of aquatic community and functional structure. To maintain high species diversity in Great Lakes sand dunes ecosystems we promote protection for both forest and dune habitat to safeguard unique species and biological traits that use interdunal wetlands.

Keywords Functional Richness · Great Lakes · Beta Diversity · Habitat Filtering · Community Assembly

Introduction

Understanding how biotic and abiotic conditions influence species distributions is a major theme of ecological studies and discussion (Kraft et al 2015; Cadotte and Tucker 2017). Biodiversity patterns can be evaluated at different levels of scale, from broad geographic patterns to the local scale among sampling sites. Historically these relationships have been analyzed by directly comparing taxa abundance to habitat characteristics (Chase and Myers 2011) because abundances should respond as environmental conditions change. By using traits in addition to taxonomic abundance information, connections between abundance and habitat are seen that are not always apparent using only one of these measures alone (Schulze and Mooney 1993; Flynn and Palmer 2011; Parravicini et al 2014) and may better explain distribution patterns (Boersma et al 2016). Naturally occurring gradients that encompass a diversity of habitat characteristics present opportunities to observe how communities respond to changes in biotic and abiotic conditions. Comparing communities along habitat gradients gives insight into how species richness (Werner et al 2007; Beché and Statzner 2009), functional structure (Stevens et al 2003; Pease et al 2015), or phylogenetic diversity (Angulo et al 2018) shift in response to changing conditions.

How well or poorly suited an organism is to a habitat is influenced by the traits they possess (Poff 1997), so it follows that functional structure should change along a habitat gradient just like taxonomic shifts in abundance and distribution. Local communities are assembled through local

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habitat filters and interspecific interactions. Habitat filtering refers to the collective influence of biotic and abiotic factors in shaping community composition and structure (Diamond 1975) emphasizing the importance of niche-related mechanisms. Dispersal limitation mechanisms state that species fail to reach suitable habitat due to geographic distance or other dispersal barriers (Hubbell 2001), which creates variation in species diversity across space. The relative importance of assembly mechanisms is difficult to disentangle, context-dependent in aquatic systems (Vorste et al 2021) and both processes may act together (Belyea and Lancaster 1999) to drive community composition and diversity.

Environmental gradients have long been used to identify the factors driving community assembly. There is a distinct natural vegetation gradient present in the Laurentian Great Lakes freshwater dune system that has been established over the last several thousand years characterized by early, desert-like environments near lakeshore to older, lush deciduous forests inland. This open-forested dune gradient represents a vegetation succession gradient from little to no vegetation, to grasses to shrubs to pines, to mixed forest of trees, and an environmental gradient of increasing organic matter, soil chemistry (pH), and canopy cover (Cowles 1899; Jackson et al 1988; Lichter 1998).

The succession of vegetation communities is well established (Cowles 1899; Olson 1958), however the likely concomitant changes in the biological community in wetlands embedded along the dune gradient have not been investigated. Between dune ridges in the low swales lie wetlands (hereafter, interdunal wetlands) that fall on a gradient characterized by aquatic vegetation (Jackson et al 1988) that suggests wetland communities experience a dramatic shift in potential habitat filters (DeVries-Zimmerman et al. 2018). Previous work has shown interdunal wetlands occurring in open dune habitat show strong hydrological connectivity to Great Lakes water level (Comer and Albert 1993), receive high solar radiation, have sandy substrate with low organic content, sparse aquatic vegetation (Jackson et al. 1988; Smith et al. 2008)), and little to no potential for allochthonous input (Lichter 1998). Wetlands occurring further inland in forested dune habitat have drastically different environmental conditions: hydrology largely independent of Great Lake levels (Comer and Albert 1993), organic-rich sediment (Smith et al 2008), abundant aquatic vegetation, and woodland vegetation surrounding each wetland (Lichter 1998) providing comparatively immense amounts and diversity of basal trophic resources relative to open dune wetlands. The dune succession gradient may exert strong controls on the taxonomic and trait composition of aquatic communities.

Canopy cover is a main gradient in the dune ecosystem. The distribution, abundance, and diversity of freshwater aquatic communities are strongly correlated with forest canopy cover (Skelly et al 1999; Bischof et al 2013). Wetlands with higher canopy cover have been linked to decreased snail species richness (Hoverman et al 2011), decreased insect abundance (Palik et al 2001), and lower insect flux to the surrounding terrestrial habitat (Schriever et al 2014). Hydrology, tree canopy, substrate, and aquatic vegetation have been found to influence community composition in rivers (De Nadaï-Monoury et al 2014; Majdi et al 2015) and wetlands (Moreira et al 2010; French and McCauley 2018) for both amphibians and insects. Likewise, environmental factors may have similar influence on trait structure and diversity. Macroinvertebrates have a broad spectra of dispersal strategies, life history characteristics, and trophic strategies, and are ubiquitous in fishless systems. Canopy cover informs adult dragonfly habitat selection and may reduce visitation (Binckley and Resetarits, 2009; French and McCauley 2018), whereas presence of leaf litter and aquatic macrophytes contribute to different trophic strategies (Heino 2008). Harsh open dunes could promote taxa with active dispersal mechanisms to dominate interdunal wetlands and passive dispersal, either aquatic or aerial, in forest late successional wetland habitat because wetlands might have longer permanence (Schriever and Lytle 2016). Aquatic invertebrate dynamics across the dune succession gradient is unexplored, yet offers an excellent opportunity to examine how environmental changes and distance along a succession gradient can drive taxonomic and functional changes in a community.

The Great Lakes coastal dune system has a pronounced environmental gradient within a geographic area small enough to hold a shared species pool, offering a unique natural experiment to test the role of a succession gradient on invertebrate community assembly. We used two forms of evidence to assess habitat filtering in this study: taxa abundance shifts and trait abundance shifts along environmental gradients. In this study we sampled macroinvertebrates from wetland communities across the open dune (nearer to Lake Michigan shoreline) to forested dune (inland) gradient to assess the relative importance of habitat conditions in structuring taxonomic and functional community composition. We characterized the wetland environmental conditions along the open-forested dune succession gradient and hypothesized that surrounding vegetation density (canopy), proportion of aquatic macrophyte coverage, and distance from Lake Michigan would structure trait and taxa distributions. We investigated how taxonomic diversity, functional richness, and abundance change along the open-forested dune gradient. We hypothesized that wetlands in forested dune habitat would harbor richer and more diverse communities in terms of traits and taxa observed due to wider potential niche availability and less harsh environment.

In addition to understanding how conditions related to the dune succession gradient influenced macroinvertebrate community structure, we evaluated the influence that physical distance had on community and functional structure. We tested whether wetlands with similar vegetation were more similar in species composition to each other regardless of physical distance from one another. We predicted that dissimilarity in taxonomic composition would increase both with distance between wetlands and in dissimilarity of surrounding terrestrial vegetation. If the dune succession gradient is the dominant driver, then general patterns of community structure should be shared in interdunal wetlands that share the same dune successional habitat, even if spatially distanced. If dispersal drives community composition, we should see aquatic macroinvertebrate communities becoming more dissimilar the farther apart wetlands are from one another regardless of dune habitat. Determining the ecological parameters that regulate community assemblage patterns in interdunal wetlands will fill a critical gap in our understanding of these rare wetland ecosystems and their role in the greater dune ecosystem.

Methods

Study Site Description

Ludington State Park (LSP; Ludington, Michigan) contains 5,300 acres of sand dunes, Lake Michigan shoreline, wetlands, and forest. The state park is adjacent to the Nordhouse Dunes Wilderness Area, and together these two protected areas constitute the largest concentration of freshwater interdunal wetlands worldwide (Chapman et al 1985). We sampled 11 fishless interdunal wetlands within a 3 km^2 area in the state park. We randomly selected wetlands that were distributed among the dune succession gradient running longitudinally from the Lake Michigan shore in open dune ($n = 6$ wetlands) to inland forested dune habitat ($n = 5$ wetlands; Fig. 1) and were accessible by foot. The average distance between wetlands was 1198.05 m (range: 96.85–2116.89 m).

The open-forested dune succession gradient was quantitatively measured with remote sensing and GIS applications on 2018 aerial imagery acquired from National Agriculture Imagery Program (NAIP). A supervised Object-based image analysis (OBIA) classification was performed on the study area. After wetlands and vegetation were determined, a 100-m buffer was created extending from the boundaries of the 11 study wetlands. The area of vegetation that fell within the buffers were summed to get the surrounding vegetation area values in square meters. Using the area of the buffers and summed area of surrounding vegetation, the percentage of surrounding vegetation was calculated. The percentage represents the proportion of buffers that are intersected by the vegetation, where 0 is no vegetation to 100 completely vegetated.

Aquatic Macroinvertebrate Collection

We collected macroinvertebrate community samples once per month from April to October 2017 using a 550 µm D-frame dipnet. Dipnet effort was based on a 1 s/m^2 sweeping effort through surface, middle, and benthic water column layers in all available microhabitats (vegetated and non-vegetated). We adjusted the sampling effort time based on wetland size (wetlands smaller than 30 m^2 were sampled for at least 30 s and wetlands larger than 300 m^2 were

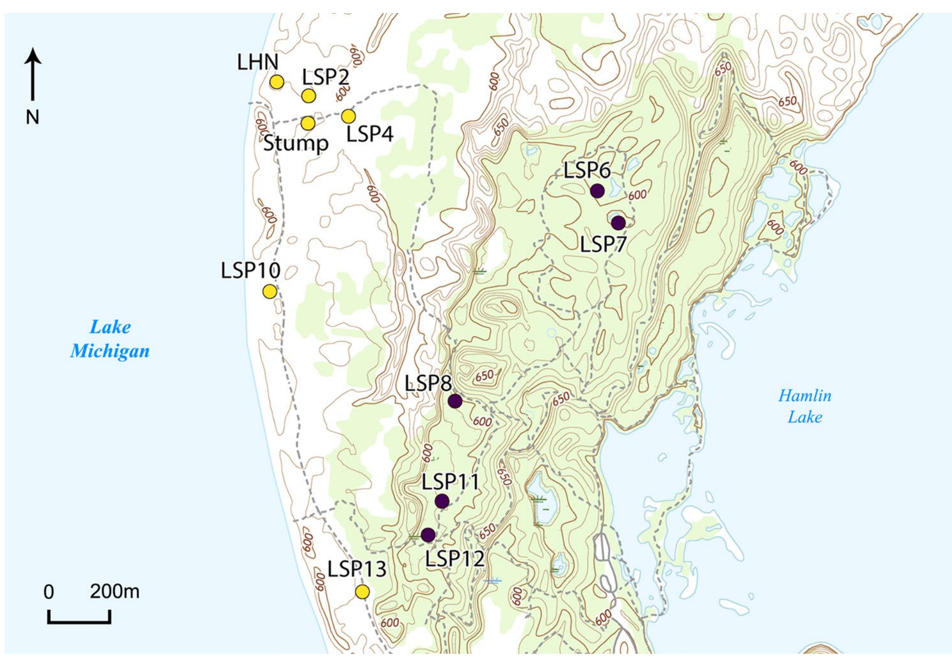

Fig. 1 Topographic map of study sites in Ludington State Park, Ludington, Michigan. LHN, LSP2, Stump, LSP4, LSP10, and LSP13 are interdunal wetlands in open dune habitat (white areas, yellow dots) and LSP6, LSP7, LSP8, LSP11, and LSP12 are interdunal wetlands in forested habitat (green areas, purple dots). J. Glatz, Western Michigan University Libraries. Source map: USGS

limited to 5 min of sampling) and aquatic vegetation coverage to reduce the impact of repeated sampling events and work effectively within dense vegetation to ensure enough time was spent actively sweeping. Collected samples were preserved in 80% ethanol. In the laboratory, each preserved sample (n = 77) was sorted, identified, and counted using a dissecting microscope. We identified the majority of macroinvertebrates to genus level, with the exceptions of some Diptera and Mollusca to family-level and subclass-level for Collembola and Annelida using a variety of keys (Wiggins 2000; Merritt et al., 2008; Perez and Sandland 2014; Bright 2016; Bright and O'Brien 2017). A list of identified taxa is available online in a KNB repository (https://doi.org/10.5063/F1P26WK0). Monthly taxa abundances per wetland were averaged across the study period.

Habitat Data Collection

During each sampling trip, we measured instantaneous dissolved oxygen (DO, mg/L), pH, temperature (°C), salinity (ppt, YSI Professional Plus, Yellow Springs, OH), and water depth at the deepest point, and estimated aquatic vegetation coverage at each wetland. We visually estimated aquatic vegetation cover percentage separately for each vegetation type (i.e., submerged, floating, emergent) from the shoreline during each sampling trip, and summed those values to get an estimate of total aquatic vegetation coverage (KNB https://doi.org/10.5063/F1P26WK0). Monthly measurements were averaged across the study period.

Functional Trait Data Collection

We amassed trait information from an assortment of published trait databases, primary literature, identification guides, and textbooks for taxa that constituted more than 0.01% of the total abundance (> 4 individuals). This cut-off was mainly due to lack of published life history information of numerically rare taxa. Each taxon was represented by a combination of traits, known as its functional trait niche (FTN) (Poff et al 2006). Functional trait diversity was represented by a species x trait matrix for 73 taxa with complete trait information. Five traits: functional feeding guild (FFG), dispersal strategy (Disp), voltinism (Volt), length of aquatic life cycle stages (AqStg), and the proportion of the life cycle spent in aquatic habitats (AqLife) (total 18 modalities/states) were selected a priori for consideration based on presumed differential advantage across the studied habitat gradient and availability of trait information in the literature (Table S1 and KNB https://doi.org/10.5063/F1P26WK0). FFG is important to ecosystem functioning and the remaining traits are associated with temporary or frequently disturbed habitat (Heino 2008; Batzer and Boix 2016).

Data Analysis

Assessing Macroinvertebrate Diversity

Diversity estimates were obtained using the online software iNEXT-4steps (Chao et al 2020). We realize not all habitats were sampled equally well, not all species are easily detected, and detection probabilities change across sites (Chao and Chiu 2016), so we calculated sample completeness and obtained diversity estimates adjusted for unequal sample sizes and imperfect detection of rare species (Chao et al. 2020) in order to assess sampling effort and make fair comparisons among multiple wetland assemblages. Diversity estimates based on Hill numbers were calculated by a non-asymptotic coverage-based rarefaction for taxa richness ($q = 0$), asymptotic estimation for Shannon diversity ($q = 1$), and Pielou evenness (100 bootstraps; Pielou 1969) using abundance data pooled across months within each wetland (Table 1). The maximum coverage (C_{max}), or maximum level at which samples can be compared, is calculated as the minimum coverage achieved after doubling (extrapolating) the size of the smallest observed sample (Chao et al. 2020). Because taxa richness estimates were achieved via a non-asymptotic method, undetected taxa richness represents minimum non-detection (Chao et al. 2020).

We performed all statistical analyses in RStudio statistical software version 4.0.0 (R Core Team 2020). Functional richness was calculated for each wetland assemblage and describes the amount of functional space occupied by a given community, which allows us to compare niche breadth between communities (Mouillot et al 2005). Functional richness was calculated in the FD package with the function dbFD (Laliberte et al. 2014) on the traits x taxa abundance matrix, which was created by cross-multiplying the site x taxa abundance matrix with taxa x trait matrix.

We assessed longitudinal gradients in environmental variables and diversity metrics along the open-forested dune gradient with regression models. Many habitat variables were correlated; (1) mean water temperature was positively correlated with DO and salinity (Pearson $r > 0.7$); (2) average total aquatic vegetation was positively correlated with average submergent ($r = 0.87$), average floating ($r = 0.56$), average emergent vegetation ($r = 0.66$) and inherently connected because individual variables make up the total aquatic coverage and (3) terrestrial vegetation also expressed positive collinearity with distance from Lake Michigan shore ($r = 0.79$), showing an increase in a logistic manner toward an asymptote around 500 m from Lake Michigan. Therefore, we first ran a Principal Component Analysis (PCA) using prcomp function in vegan package v2.5–6 (Oksanen et al 2018) on standardized habitat variables to collapse them into informative axes and then computed linear univariate regressions between diversity metrics and the most informative axes

Table 1 Observed and estimated species diversity for orders q = 0 and 1. Data sufficient to asymptotically estimate Shannon diversity (q = 1), but asymptotic estimates represent only the lower bound for taxa richness (q = 0). Taxa richness and Pielou J' estimated by coverage-based rarefaction and extrapolation and compared for equally complete samples (C_{max})

	Sample completeness		Taxa richness q = 0		Shannon diversity q = 1		Evenness	Abundance	Functional richness
	q = 0	q = 1	Observed	Estimated	Observed	Estimated	J'		
Open dune									
LHN	0.875	0.997	28	30.49	4.02	4.06	0.409	1617	37.92
LSP2	0.917	0.999	22	22.42	2.839	2.849	0.336	3459	42.49
Stump	0.694	0.997	25	30.63	2.9387	2.9585	0.316	2776	73.39
LSP4	0.848	0.997	39	42.26	7.4498	7.5019	0.537	3513	83.62
LSP10	0.794	0.999	27	28.45	2.807	2.8165	0.309	5437	69.36
LSP13	0.862	0.999	56	55.89	11.66	11.72	0.611	7222	101.32
Forested dune									
LSP6	0.846	0.997	66	73.09	13.508	13.66	0.608	3606	99.67
LSP7	0.918	0.998	67	69.22	11.4797	11.57	0.576	4825	98.99
LSP8	0.875	0.997	49	53.17	11.39	11.53	0.614	2270	98.84
LSP11	0.937	0.999	59	60.01	10.33	10.40	0.571	5074	99.66
LSP12	0.929	0.998	26	26.88	4.88	4.91	0.482	2278	82.55

from the PCA. We computed quadratic regression models to quantify the relationship between PC1 and evenness and functional richness because relationships were non-linear. GLM tested the effects of distance from lakeshore (also representing terrestrial vegetation) on the abundance of macroinvertebrate assemblages using a Poisson distribution.

Macroinvertebrate Community Patterns

We performed a redundancy analysis (RDA) to identify the habitat explanatory variables (unscaled temperature, wetland depth, pH, aquatic vegetation coverage, and terrestrial vegetation percentage) explaining the variation in the macroinvertebrate community (Hellinger transformed species abundance) with significance assessed by permutation (number of permutations: 999). Hellinger transformation followed by RDA produces good representations of species and sites, little horseshoe effect, and preserves distance along gradient (Legendre and Gallagher 2001). Results of the ordination were displayed in correlation triplots (scaling 2) with species scores. Similarly, we performed a separate RDA to gauge influence of explanatory habitat conditions on functional traits with significance assessed by permutation (number of permutations: 999).

We conducted Mantel and partial Mantel tests to clarify whether community patterns were more likely driven by dispersal and/or environmental filtering using the ade4 package v1.7–18 (Dray and Dufour 2007). We constructed wetland distance, wetland community dissimilarity, and vegetation dissimilarity matrices for the analyses. We calculated distance between wetlands with Haversine distance of UTM coordinates. Bray–Curtis dissimilarity (distance) was calculated on taxa abundance and vegetation dissimilarity was calculated separately as the Euclidean distance of terrestrial and aquatic vegetation cover. We checked for spatial autocorrelation among vegetation and geographic distance matrices with mantel tests at 999 Monte Carlo replicates. Three Mantel tests assessed whether community composition between wetlands were correlated with 1) spatial location of each wetland, with 2) differences in total aquatic vegetation and 3) with differences in terrestrial vegetation. We completed partial Mantel tests to isolate effects of vegetation (environmental filtering) and distance (dispersal) on community dissimilarity while removing the influence of geographic distance. Four partial Mantel tests were conducted to: 1) test the correlation between community dissimilarity and terrestrial vegetation dissimilarity while controlling for geographic distance, 2) test the correlation between community dissimilarity and aquatic vegetation dissimilarity while controlling for the influence of geographic distance, 3) test the correlation between community dissimilarity and geographic distance while controlling for terrestrial vegetation dissimilarity, and 4) test the correlation between community dissimilarity and geographic distance while controlling for aquatic vegetation dissimilarity.

Results

Over the course of our 7 monthly sampling events, we collected 42,246 individual organisms from the 11 wetlands, representing 92 unique taxa and 47 families with 9 taxa unique to 5 wetlands (KNB https://doi.org/10.5063/F1P26WK0). Taxa richness among wetlands ranged from 22–70 observed taxa and 23.5–85.2 estimated richness (Table 1). Alpha diversity was highest in LSP7 (Forested dune) based on observed taxa and LSP6 (forested) based on estimated taxa richness. Only Chironomid midges, *Ischnura* damselflies, *Sympetrum* dragonflies, and Notonectid backswimmers were found at every wetland. The macroinvertebrate assemblage in LSP showed a few taxa comprise the majority of the individuals. The wetlands were dominated by Diptera in terms of abundance (53% of total abundance) and richness – 18 taxa, despite many groups only being identified to family level. Chironomid midges were the most abundant taxa, representing ~30% of total collected individuals. Thus, we had many rare species, for example 5 taxa were collected only once throughout the entire sampling period and most taxa (80) constituted less than 1% of total abundance, while only a few taxa were common and abundant. To visualize this (Fig. 2) we present the 32 taxa that had site abundance of at least 1% of wetland site total over the collection period. Abundance patterns show some taxa are abundant across all sites (Chiro) while other taxa are abundant in only to two wetlands (Aedes mosquitos) and that patterns in abundance differ between wetlands in open dune vs wetlands in forested dune habitat.

Dune Succession Gradient

Environmental conditions (Fig. 3) were variable and invertebrate diversity patterns changed across the dune succession gradient. Principal components analysis showed that 50% of the habitat variation was explained by the first component (PC1: Online Resource Table S2, Fig. S1). Temperature, DO, salinity, and pH had similar, negative loadings on axis 1, indicating that higher values on PC1 correspond to lower values of these water quality measures. Lake distance and terrestrial vegetation had high positive loadings, meaning sites farther from Lake Michigan also had more surrounding terrestrial vegetation. This gradient cleanly separated open dune (LHN, LSP2, Stump, LSP10, and LSP13; negative loadings on PC1) and forested dune (LSP6, LSP7, LSP8, and LSP11: positive loadings on PC1) wetlands. PC2 accounted for 25% of the variation and water depth, submerged vegetation cover, and total aquatic vegetation cover had moderately high positive loadings. Floating and emergent vegetation were of low importance on both axes.

Water conditions, distance to lake, and amount of terrestrial vegetation (PC1) showed significant, positive relationships with estimated taxa richness and Shannon diversity ($p=0.006$, $R^2=0.53$, $p=0.004$, $R^2=0.59$, respectively) and significant quadradic relationships with functional richness and evenness ($p=0.01$, $R^2=0.6$; $p=0.\ 005$, $R^2=0.66$, respectively; Online Resource Table S3, Fig. 4), while PC2 (aquatic vegetation and depth) was only significant with abundance ($p=<0.0001$; Online Resource Table S3). LSP12 had high terrestrial vegetation cover, low aquatic vegetation, and lower than average dissolved oxygen and considerably lower, richness, diversity, and evenness compared to other wetlands with similar terrestrial vegetation coverage. Functional richness generally increased with increased terrestrial vegetation but was highest in LSP13 wetland with high aquatic vegetation coverage and low terrestrial vegetation.

Community Composition Patterns

We observed variation in macroinvertebrate community structure in response to environmental conditions. The RDA showed the habitat variables explained 79% of the variation in the species abundance data (adjusted $R^2=0.586$, $p=0.001$, Online Resource Table S4). The first axis (RDA1, $p=0.002$) accounted for 64.5% of constrained variance. Terrestrial vegetation on RDA1 separated the open dune from forested dune habitat and was directly opposed by water temperature and pH, where open dune wetlands are warmer and have higher pH and forested dune wetlands are on average cooler with lower pH (Fig. 5a). Aquatic vegetation had similar positive loadings on both axes. The second axis explained 20% of constrained variance, but was not statistically significant (RDA2 $p=0.10$). Average water depth and average total aquatic vegetation loaded highest on RDA2 followed by a moderate, positive loading from average water temperature.

The RDA ordination for macroinvertebrates revealed differences in community composition among wetlands and habitat conditions. LSP13 and LSP11 were similar in average depth

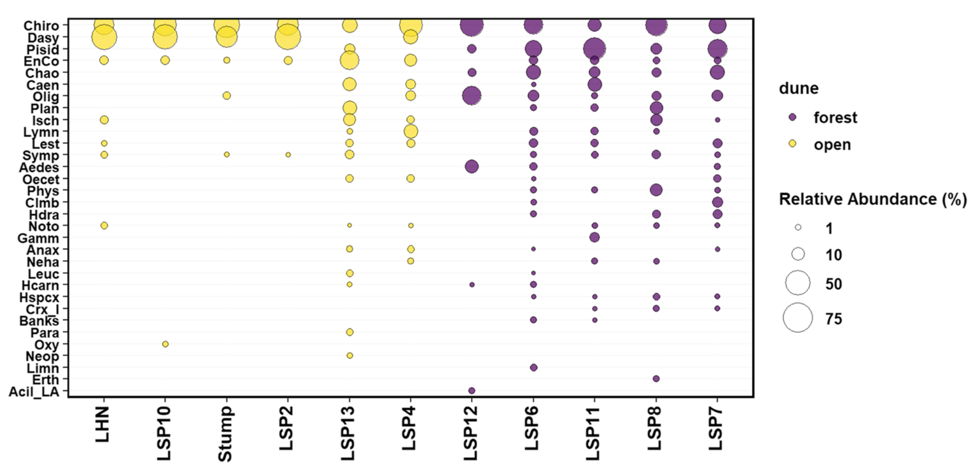

Fig. 2 Figure shows the 32 taxa that had at least 1% abundance of wetland total abundance over the collection period. The size of the points indicates relative abundance and colored by dune habitat. Refer to Online resource Table S3 for complete list of taxon names

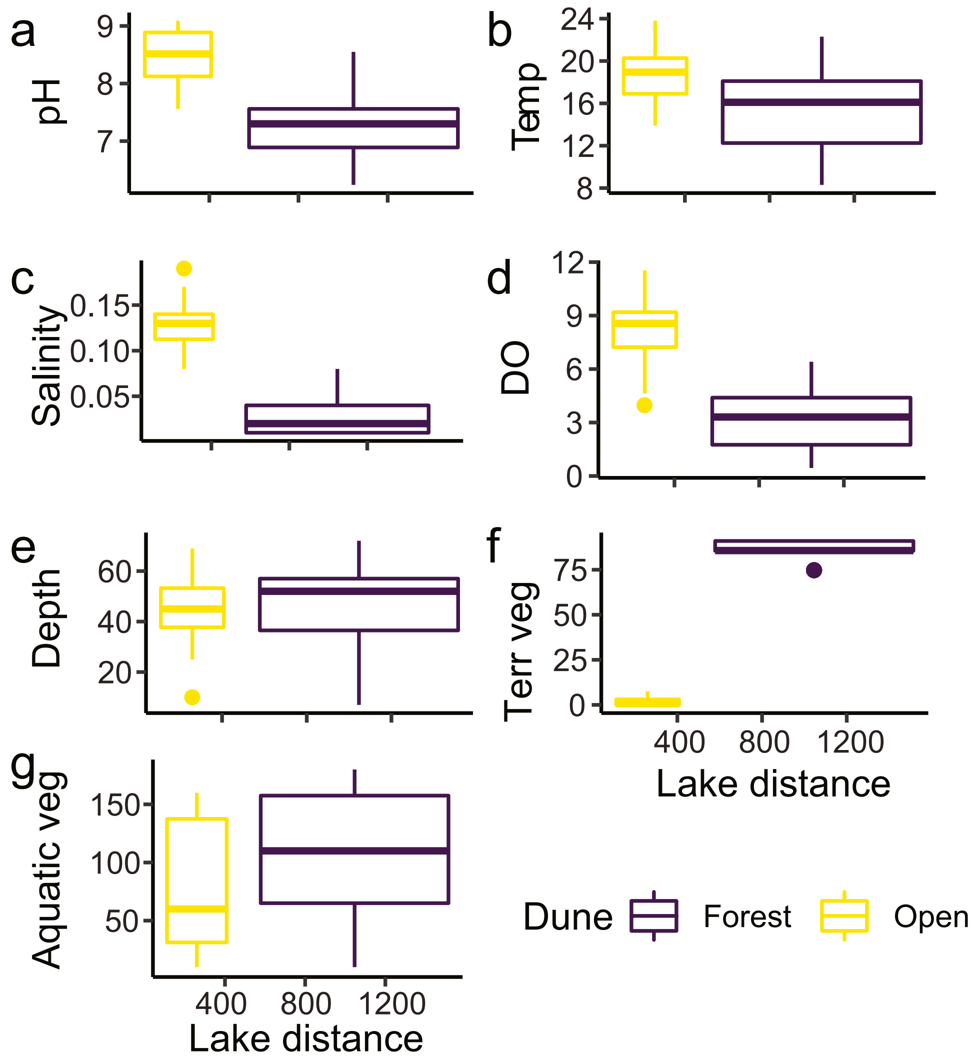

Fig. 3 Boxplots showing variation in environmental variables across dune succession gradient spanning from near lakeshore to forested back dune. Data is colored by dune group

and average total aquatic vegetation coverage, but LSP11 was on average 3 degrees cooler with a nearly closed canopy compared to LSP13 with an open canopy, thus placing them near each other in the ordination, yet in distinct wetland groups. Pisidiidae clams were overwhelmingly collected from forested dune wetlands with high aquatic vegetation coverage which was highest in LSP8, whereas, *Dasyhelea* (Diptera: Ceratopogonidae) were found in high numbers in wetlands LSP10, LSP2, LHN, and Stump which have little aquatic vegetation and higher average water temperature and pH (> 8.5) in open dune interdunal wetlands (Fig. 5a). Chironomidae midges had highest abundances in open dune wetlands LSP10 and Stump. Wetlands LSP6, LSP7 and LSP8 were characterized by heavy terrestrial vegetation cover (forested dune), high *Chaoborus* (Diptera: Chaoboridae) abundance, and lower average water temperature and pH. *Culex*, *Aedes*, and *Uranotaenia* mosquitoes were only found in forested dune wetlands with highest abundances in LSP12. LSP13 was characterized by on average deeper and warmer water, higher amounts of aquatic vegetation, almost no surrounding terrestrial vegetation, and high taxa richness (estimated 55.88) and was directly opposed by LSP12 which had on average shallow and cool water, with little aquatic vegetation surrounded by heavy terrestrial vegetation, low taxa richness (estimated 26.88) and high abundance of Oligochaete worms. Overall, taxonomic abundances were more dissimilar between wetlands of different dune groups (open vs forest, mean Bray–Curtis dissimilarity = 0.65) than comparisons within dune groups (open mean BC = 0.51; forest mean BC = 0.50).

Mantel tests were performed to evaluate the relative influence of the environmental and geographical distances on community similarity. We predicted wetlands will be more similar in species composition if they share the same dune succession habitat regardless of physical separation among wetlands. As wetlands became physically more separated, their corresponding invertebrate communities also became more dissimilar ($r = 0.4946$, $p = 0.005$; Online Resource Fig. S2). Aquatic vegetation was not spatially autocorrelated ($r = 0.0526$, $p = 0.259$), but terrestrial vegetation was

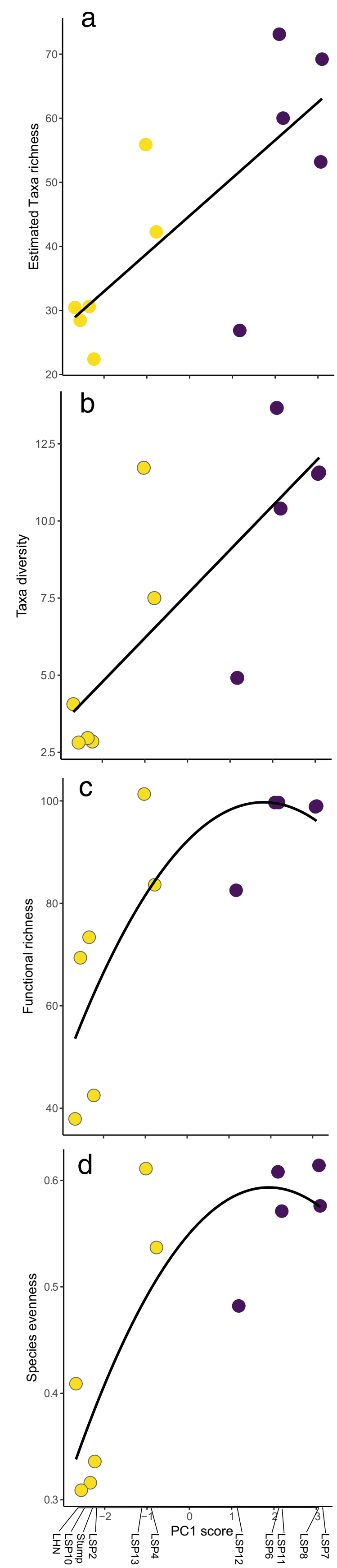

Fig. 4 Statistical relationships between diversity metrics **a**) estimated ▸ taxa richness, **b**) observed Shannon diversity, **c**) functional richness, **d**) taxonomic evenness and PC1. Colors separate wetlands by dune group (yellow = open dune, purple = forested dune). Higher values on PC1 correspond to wetlands with lower water temperature, DO, salinity, and pH values, and are farther from Lake Michigan with more surrounding terrestrial vegetation. Refer to Online Resource Table S2 for model output

(r = 0.309, p = 0.039; Online Resource Fig. S3). Terrestrial vegetation showed a strong correlation with invertebrate community dissimilarity (r = 0.5188, p = 0.005), indicating interdunal wetlands had more different taxa assemblages as the terrestrial vegetation composition around the wetlands became increasingly different. Total aquatic vegetation dissimilarity had a weak, but significant positive correlation with the community Bray–Curtis dissimilarity matrix (r = 0.2772, p = 0.044). The partial Mantel tests accounting for spatial autocorrelation confirmed the importance of both terrestrial and aquatic vegetation (habitat filtering) driving community composition (r = 0.4248, p = 0.019; r = 0.3298, p = 0.028, respectively). However, there were significant positive correlations between community dissimilarity and distance between ponds while accounting for terrestrial vegetation dissimilarity (r = 0.432, p = 0.005) and between community dissimilarity and distance between ponds while controlling for aquatic vegetation dissimilarity (r = 0.5721, p = 0.002), indicating spatial factors (dispersal) play a role in macroinvertebrate community structure as well. The difference in terrestrial vegetation around wetlands is stark; either wetlands are very dissimilar or not and distance between wetlands doesn't necessarily indicate dissimilarity in terrestrial vegetation (Fig. 6).

Trait Structure Patterns

We performed a redundancy analysis (RDA) to test for the influence of habitat factors on trait structure. Traits associated with interdunal wetlands in open dunes tended to group separately from wetlands in forested dune habitat. The RDA for traits suggested habitat variables (R^2_{adj} = 0.25, p = 0.15) explained 62.7% of the total variance observed. Axis 1 (RDA1) was not significant (p = 0.25), yet accounted for 34.5% of total variance explained (55% of constrained). Most of the variation on RDA1 was associated with two opposing responses, average water temperature and terrestrial vegetation coverage (Fig. 5b). Species that are partially aquatic spending less than a year in the water, are aerial active dispersers, and have bi/multi-voltine life history (AqLife1, Aqstg1, Disp4, and volt3) were more pervasive in open dune wetlands with higher average water temperature and low terrestrial vegetation cover. Mosquitos, which are known poor dispersers were collected only in forested dune

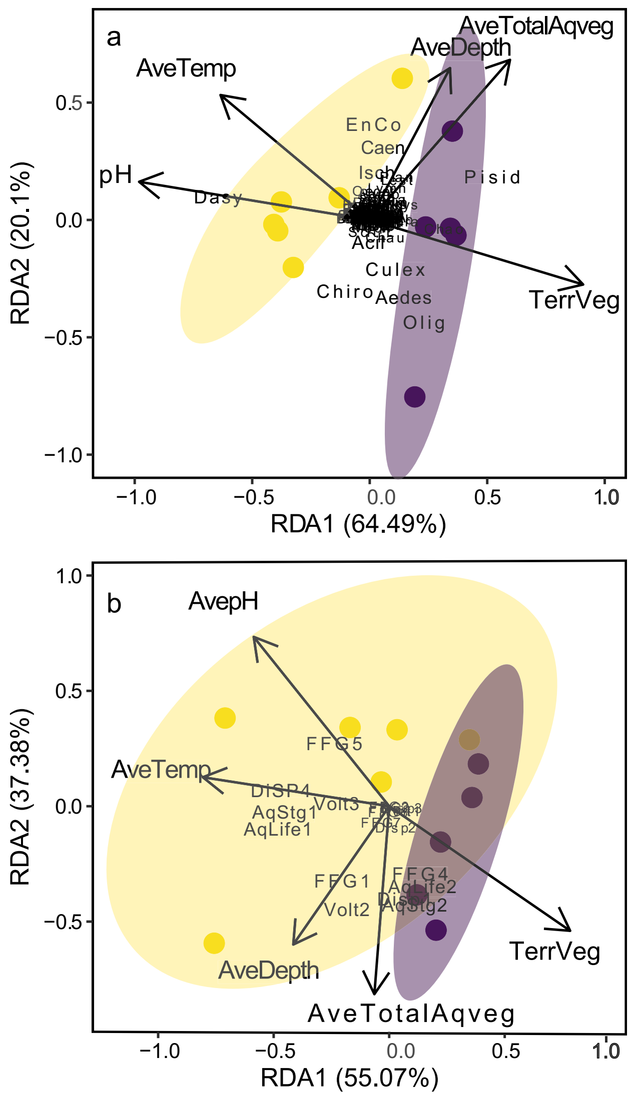

Fig. 5 RDA triplot for **a**) taxa and **b**) traits. Colors separate wetlands by dune group (yellow = open dune, purple = forested dune) and each dot is a wetland. Refer to Online resource Table S3 for complete list of taxon scores and Table S1 for trait abbreviations

wetlands. RDA axis 2 explained 37% of the variation in the trait-habitat relationship and was most strongly associated with average water depth and total aquatic vegetation variables with some contribution from terrestrial vegetation which was opposed strongly by pH. Taxa that are characterized as entirely aquatic spending more than 1 year in aquatic habitats, are collector-filterers, and/or are aquatic passive dispersers (Aqlife2, Aqstage2, Disp1, and FFG4) were correlated with deeper wetlands with more aquatic vegetation. Taxa that were predators and/or those with univoltine life histories were present in most habitats and not pulled strongly to one habitat over another. The permutation test based on all constrained eigenvalues indicated RDA2 was not significant ($p = 0.15$). Traits were more dissimilar between wetlands of different dune vegetation groups (open vs forested; mean Bray–Curtis dissimilarity = 0.42) than comparisons within dune groups (open mean BC = 0.35; forest mean BC = 0.29). This suggests that functional traits of macroinvertebrates differed between wetlands in the open and forested dunes.

Discussion

The Laurentian Great Lakes coastal dune system has a pronounced environmental gradient, offering a natural experiment to test the role of a dune succession gradient on aquatic invertebrate community assembly. This habitat gradient, especially surrounding terrestrial vegetation and water quality parameters, proved influential on the presence and pattern of taxa and functional traits, as well as community-level characteristics such as diversity and richness of the aquatic macroinvertebrate community in interdunal wetlands.

Diversity Pattern Across Dune Succession Gradient

Macroinvertebrate diversity metrics and functional richness increased with distance from the lakeshore as did the amount of surrounding terrestrial vegetation, thereby showing evidence for predictable changes along the dune succession gradient. Other studies have shown plant species richness and diversity (Zhang et al 2005) and bird richness and density (Van Orman 1976) gradually increase with succession and high vegetation species turnover (Lichter 1998), while others have shown plant species richness peaks at intermediate levels of environmental and disturbance factors along a coast-to-inland gradient (Isermann 2005; Peyrat and Fichtner 2011). Isermann (2005) showed terrestrial vegetation and soil interact along a dune gradient causing soil pH to increase in acidity moving inland. In our study the amount of terrestrial vegetation surrounding interdunal wetlands and water acidity increased with distance from the lakeshore. In addition, wetlands in the forested dunes had higher variation in environmental condition (water temperature, DO, pH, salinity, water depth) and higher taxa richness and diversity between wetlands. Higher environmental variability has been associated with higher biodiversity because it promotes niche differentiation, which allows more species to coexist (Chesson 2000; Amarasekare 2003; Peláez et al 2017). These differences created a dramatic gradient within a single ecosystem type over a short geographic distance. Our study found different taxa and functional traits varied in dominance along the dune succession gradient indicating habitat filtering by

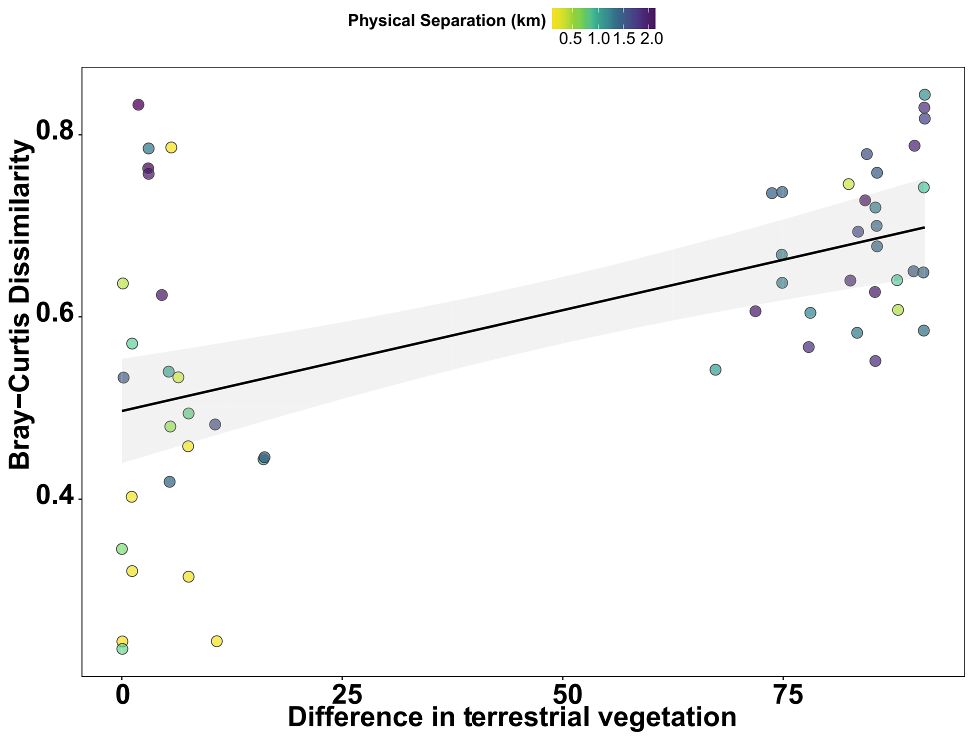

Fig. 6 Plot of pairwise comparison of macroinvertebrate community dissimilarity and differences in percent terrestrial vegetation cover with the geographic distance separating the wetlands overlain. Each point in the pairwise scatter plot represents the difference between two samples

changing vegetation and wetland water condition leads to species replacement and is a significant factor for community organization.

We found a strong difference in trait selection associated with life history, dispersal, and functional feeding traits across the dune succession gradient, likely the result of changes in vegetation coverage and habitat condition. We found aerial active dispersers associated more with interdunal wetlands nearer lakeshore in the open dunes and aquatic passive dispersal was associated with wetlands in forest farther from Lake Michigan. The dynamic nature of interdunal wetlands could explain the high abundance of active dispersers, especially chironomid midges, *Dasyhelea* biting midges, and Odonates. Active dispersal would be advantageous and confer resilience in a frequently disturbed or temporary habitat, such as the open dunes. Multivoltism was also associated with interdunal wetlands, which is congruent with findings from intermittent ponds and streams (Schriever and Lytle 2016), a similarly dynamic habitat. We identified diverse Coleoptera beetle (although low abundance), Trichoptera caddisfly assemblages, and abundant Pisidiidae fingernail clams (fully aquatic) in wetlands in the forested dunes, illustrating support of diverse feeding guilds especially guilds dependent on vegetation, leaf litter, and organic matter particulates associated with breakdown of litter.

We expected many aquatic species to exhibit a high degree of spatial variability in their distributions in response to the rather harsh and variable environmental conditions of the freshwater coastal dune system. We show interdunal wetland communities that experience similar terrestrial vegetation are more similar in invertebrate composition versus communities that are only geographically close but differ in vegetation. Mantel tests suggest both habitat filtering and dispersal play a role in determining assemblage structure in interdunal wetlands at Ludington State Park. Terrestrial vegetation was spatially autocorrelated, indicating a predictable pattern in space: sites close to each other tended to be similar, while distant wetlands tended to be different in terrestrial vegetation. Turnover beta diversity (i.e., change in community structure along an environmental gradient; Anderson et al 2011) is predicted to decline along a gradient of low to high disturbance (i.e., pond permanence in Chase 2003), a gradient of distance from wetlands spaced far apart to closer to one another (Nekola and White 1999; Chase 2003), and gradient of habitat complexity or environmental variation. The prediction is sites near each other should have similar species composition and that sites farther apart should have more dissimilar species compositions due to separation in space (Nekola and White 1999). In this study we show both aquatic habitat and dispersal help explain patterns of aquatic macroinvertebrate community structure in interdunal wetlands. Terrestrial and aquatic vegetation are significant after controlling for the effect of space, but spatial location is also a driver in community composition when controlling for vegetation. Studies have suggested the relative role of filtering and spatial processes along environmental gradients in aquatic systems may be context dependent (Vorste et al. 2021) and both mechanisms may operate simultaneously. In our case wetlands in the freshwater sand dune ecosystem host diverse aquatic biodiversity that is variable across the dune succession gradient, which is useful to recognize for conservation and protection of rare habitats (Cadotte and Tucker 2017).

We show macroinvertebrate assemblages exhibited turnover beta diversity (dissimilarity) across the dune succession gradient from sparsely vegetated to forested dune habitat. LSP13 and LSP4 wetlands are situated near the forest line and had considerable aquatic vegetation growth compared to other interdunal wetlands in the open dunes. The presence of aquatic vegetation offered increased trophic diversity and habitat complexity that was unique among the open-dune wetlands, increasing niche availability and subsequently taxonomic diversity relative to nearby wetlands. LSP12 had dense canopy cover, the least amount of aquatic vegetation of all wetlands, and a thick layer of decaying plant matter on the wetland bottom. Light limitation and heavy litterfall in LSP12 fostered a community lower in functional and taxonomic richness compared to other nearby wetlands. Similarly, Chase (2003) showed higher dissimilarity in productivity between ponds related to higher aquatic community dissimilarity. This example recognizes the importance of basal resource availability and aquatic productivity on determining community structure and diversity.

We show habitat filtering influenced community assembly, yet biotic interactions may have contributed to differences in wetland species assemblages. Therefore, the observed relationship with dissimilarity in species composition with habitat variables can be interpreted as a result of the combined effects of species interactions, habitat environmental condition, and habitat complexity.

Community and Functional Response

We demonstrate gradients in terrestrial vegetation, pH, and water temperature best explained aquatic community composition and differentiated wetlands groups. Our results compliment what is known about the physical nature of the dune succession gradient and revealed, as far as we know for the first time, the aquatic macroinvertebrate community and functional structure change along the habitat gradient creating distinct communities.

At the functional trait level, wetlands showed differences in trait composition driven by differences in resource type and availability, and habitat heterogeneity. We found interdunal wetlands in the open dunes support high abundances of collector-gatherers (Chironomidae and *Dasyhelea* biting midges) that consume fine particulate organic matter (FPOM) and algae, and modest predator assemblages (Dytiscidae, Odonata) that consume zooplankton and/or invertebrate larvae. Forested dune wetlands are more densely vegetated, therefore opening macrophyte and detritus dependent trophic strategies (such as scrapers and herbivores) that are otherwise not available in the open dunes. Terrestrial vegetation surrounding the two habitat types varies dramatically, providing radically different allochthonous input type and amount. Open dune wetlands are surrounded by perennial dune grasses and isolated jack pines (*Pinus banksiana*) or shrubs, permitting very little terrestrial resource input (Lichter 1998), selecting against taxa that rely on those resources (i.e. shredders). Wetlands in the forested dune habitat lie in areas dominated by deciduous trees (Lichter 1998), whose leaf fall provides a vital resource for shredders and collector-filterers and -gatherers occupying these wetlands. Forested dune wetlands have substrate rich in organic matter, offering a fundamentally different niche structure compared to sandy substrate for macroinvertebrate fauna in open dune habitat (Weatherhead and James 2001; Lamouroux et al 2004). Other studies have observed similar patterns of increasing trophic diversity in multiple taxonomic groups throughout primary and secondary succession related to shifts in resource type and coverage (May 1982, Brown and Southwood 1983, Wall et al. 2002, Martinko et al. 2006, Gibb and Cunningham 2013), lending evidence that trait turnover is a general trend in communities across canopy or vegetation gradients.

In our study, we found wetlands in the open dunes and forested dunes differed in trophic and life history trait composition. Specifically, interdunal wetlands in the open dunes hosted more individuals and taxa with traits associated with desiccation resilience, faster life cycles and more generations per year, a pattern predicted and observed in intermittent aquatic habitats (Townsend and Hildrew 1994; Schriever and Lytle 2016). Interdunal wetlands do dry periodically, driven by idiosyncratic Great Lakes water levels (Albert 2007). For instance, from 1999 until 2013 water levels were relatively low (US Army Corps of Engineers 2021), leading to many open dune interdunal wetlands only holding water a portion of the year or drying completely. Lake Michigan water levels have been rising since 2013 (US Army Corps of Engineers 2021) and as a result wetlands in our study did not dry, but rather increased in depth over the course of this study (and through 2021, personal observation). Therefore, our observed trait distributions may be an artifact of hydrological selection in the past. Additionally, other traits like small body size, burrowers, and the ability to diapause may be associated with interdunal wetlands, however, we need more trait information to investigate this. If recent hydrological conditions were responsible for shaping functional community structure, we should have observed life history and dispersal traits in open dune wetlands similar to those of forested dune wetlands. However, we found open dune and forested dune wetlands differed in trophic and life history trait composition. Taxa with dispersal strategies dependent on flooding (aquatic passive) and life histories that are spent entirely in an aquatic habitat were more associated with wetlands in the forested dune habitat, suggesting frequency of drying among wetlands is variable. Forested dune communities had higher functional richness implying more occupied niche space and greater ecological redundancy which may offer greater resilience to disturbance (Hooper et al. 2005). Hydrology acting as a driver of diversity has been well documented in some freshwater communities (Wiggins et al 1980; Williams 2006; Williams et al 2007), and likely influenced functional traits and community composition in interdunal wetlands. A detailed study investigating the link between hydrology and traits is warranted.

Food web and habitat structure disparities between wetland types may also explain trait and taxonomic differences. Interdunal wetlands in open dunes appear simple; low aquatic invertebrate diversity, little to no aquatic vegetation, low nutrients amounting to limited food resources (in terms of diversity, quantity, and quality), which may contribute to dominance of a limited selection of functional feeding groups and a shorter food chain (Post 2002). Habitat complexity, including vegetation density and structure, influences community composition, availability of niches, biodiversity, mediates predation (McCoy and Bell 1991; Smith et al 2014), and may reflect higher levels of beta diversity (Hewitt et al 2005). Interdunal wetlands in the open dunes have little habitat structure for organisms to hide (except for taxa that burrower into sand, e.g., Chironomidae midges) or utilize as food resources, thereby limiting species. It would be advantageous to build food webs and quantify food chain length in wetlands along the dune succession gradient to clarify if and what role the food web plays in structuring interdunal wetland dynamics.

Species and trait composition were most different (highest variation beta diversity) in wetland pairs of open vs forested dune, illustrating the major influence of terrestrial vegetation, regardless of spatial relation, on community and trait assemblage. The influence of terrestrial vegetation on the physical and chemical condition of wetlands determines productivity (either autochthonous plant and algae growth or allochthonous leaf litter availability for base of the food web) which ultimately determine species composition. In conjunction, it is reasonable to expect that dispersal constrains the distributions of freshwater macroinvertebrates due to harsh dune environment (habitat isolation, strong winds). The combination of dispersal and different trophic pathways allows different suites of invertebrates and traits to persist in these wetlands.

Summary

To date, there is limited knowledge on the aquatic diversity in freshwater sand dune communities. Furthermore, studies that aim to elucidate patterns of diversity and the mechanisms that structure assembly on sand dunes have been mostly concerned with plant communities with the exception of a study on birds (Van Orman 1976). We sought to determine the ecological parameters that regulate community assemblage patterns and the spatial scale of similarity among interdunal wetlands. We report that taxonomic and environmental variation exists along the dune succession gradient. We found the combination of shifting terrestrial and aquatic habitat filters accounts for the structure and diversity of aquatic macroinvertebrate communities, which has provided new knowledge critical to maintaining and understanding this unique wetland ecosystem. The Great Lakes freshwater dune ecosystem is rare and threatened by development, encroachment of invasive species (Emery and Doran 2013), and changing precipitation patterns associated with climate change (Mackey 2012). Lake Michigan water levels and vegetation succession have had a profound impact on trait distributions and changes to these will have an impact on future trait and taxonomic composition. Disturbance, whether anthropogenic or natural variation in water level, could rapidly shift interdunal wetland community composition and structure.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13157-022-01596-w.

Acknowledgements We thank Jim Gallie for approving this study in Ludington State Park under Michigan Department of Natural Resources state land use permit PRD-SU-2017-019, the Ludington State Park and Big Sable Point Lighthouse staff for accommodating us during our field excursions, Jason Glatz, Western Michigan University Libraries for creating our study site map, and Claire Gilbert for calculating terrestrial vegetation density. We are enormously thankful for our field and laboratory assistants Adam Austin, Casey Doherty, Cody Boldt, Samantha Govert, Nirvisha Singh, Shakhlo Aminova, and Theo Saillant. We appreciate constructive feedback from reviewers.

Authors' Contributions CF formed research question, study design, conducted field and laboratory work, analyzed data, and wrote the manuscript. TS advised the overall research process, assisted with fieldwork and data analyses, wrote and edited the manuscript, and provided funding for this research.

Funding This research was partially supported by Michigan Sea Grant College Program, project number: R/CGLH-5, under Federal grant number: NA180AR4170102 from National Sea Grant, NOAA, U.S. Department of Commerce, and the State of Michigan awarded to TS. Research was also supported by a Research Assistantship provided by Western Michigan University awarded to CF.

Data Availability The trait data, taxa list and environmental data was deposited in the Knowledge Network for Biocomplexity (KNB). Christopher Frazier and Tiffany Schriever. Interdunal Wetland Community

(Taxonomic and Trait) and Habitat > Data 2017, Ludington State Park, Michigan, USA. Knowledge Network for Biocomplexity. https://doi.org/10.5063/F1P26WK0.

Code Availability The code used during the current study are available from the corresponding author on reasonable request.

Declarations

Conflicts of Interest Not applicable.

Ethics Approval Michigan Department of Natural Resources state land use permit PRD-SU-2017–019. This animal research only involved invertebrates and therefore was exempt from Western Michigan University IACUC (Institutional Animal Care and Use Committee) oversight.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

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