

Great Lakes coastal wetland biodiversity increases following invasive *Phragmites australis* removal

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Abstract

Invasive *Phragmites australis* subsp. *australis* is invading Great Lakes coastal wetlands and forming monocultures at an alarming rate. *P. australis* is thought to reduce wetland biodiversity both directly and indirectly through the acquisition of resources and alteration of habitat. Restoration efforts to manually remove *P. australis* at Point Pelee National Park began in 2020 and here we assess the effect of *P. australis* removal on vegetation and emerging aquatic invertebrate communities. We compared emergent vegetation and emerging aquatic invertebrate communities between a *P. australis*-invaded wetland, a *P. australis*-treated wetland, and a non-invaded wetland. We found that two-years post-restoration, vegetation species richness and the prevalence of non-*Phragmites* vegetation were both higher in the treated and non-invaded wetlands than the invaded wetland. The vegetation community of the treated wetland resembled the vegetation community of the non-invaded wetland, and the vegetation community of the invaded wetland was very different from both the treated and non-invaded wetlands. We also found that invertebrate total abundance (measured as density/m²) was highest in the treated and non-invaded wetlands, and that invertebrate abundance differed among all wetland types. Invertebrate community composition also differed among all wetland types. Manual removal of *P. australis* resulted in significant changes in both the emergent vegetation and emerging invertebrate community composition two-years following restoration.

Introduction

Wetlands are among the most important and complex ecosystems and their importance can be appreciated at local and global scales. Locally, wetlands help clean polluted water, reduce flooding, protect shoreline erosion and groundwater availability, and support biodiversity (Gibbs 1995; MEA 2005; Verhoeven et al. 2006; Mitsch et al. 2013; Mao et al. 2018). Even though freshwater wetlands cover less than 1% of the world's surface, they provide habitat to approximately 40% of known species (Ramsar Convention 2001). Globally, wetlands play major roles in carbon sequestration, coastal protection, climate control, and the maintenance of both freshwater and saltwater cycles (Ramsar Convention 2001; Gedan et al. 2001; Temmerman et al. 2013; Russie et al. 2013; Byun et al. 2018; Xu et al. 2019).

Despite the recognized importance of wetlands, 87% of global wetlands have been lost since the 18th century (Davidson 2014). The southern portion of Ontario, Canada has witnessed a devastating loss of > 68% of its freshwater wetlands since the beginning of European settlement (Penfound and Vaz 2022) and evidence of anthropogenic impacts on Lake Ontario and Lake Erie wetlands have been observed directly after European settlement, with surges of wetland loss evident within the last 200 years (Penfound and Vaz 2022). Much of the wetland loss recorded is due to anthropogenic effects, primarily development and agricultural expansion (van Asselen et al. 2013; Bradford 2016; Hu et al. 2017; Li et al. 2018). Increased development leads to pollution output, increased road density, water quality decline, and habitat fragmentation; agricultural expansion and subsequent wetland conversion alters hydrological regimes due to increased dredging, eutrophication, and nutrient overload (Roman et al. 1984; Crowder and Bristow 1988; Herdendorf 1992; Crosbie and Chow-Fraser 1999; Mitsch and Gosselink 2000; Trebitz et al.

2007; Timmerman *et al.* 2008). In addition to the threats posed by development and agricultural expansion, the introduction of invasive species into wetlands is a serious threat; one that increases with continued development (Ricciardi 2006; Calderon-Aguilera *et al.* 2012; Seebens *et al.* 2021).

Invasive species, though diverse, share similar characteristics that allow them to invade and monopolize ecosystems (Blackburn *et al.* 2011; Fei *et al.* 2014; Ruesink 2018). Mechanisms of invasion success have been observed across a variety of invasive plant species, with an emphasis on invasives within wetlands. The monopolization of limited resources is a key trait observed in invasive plants (Grime 1973; Minchinton and Bertness 2003), including the ability to dominate photosynthetic light (Kotowski and Diggelen 2004; Zedler and Kercher 2004), to influence nitrogen partitioning (Hirose and Werger 1994), to dominate growing space via size (Daehler 2003; Levine *et al.* 2003; Vilà & Weiner 2004), and through the production of standing litter (Minchinton *et al.* 2006; Holdredge and Bertness 2011). Invasive species can overcome both biotic and abiotic barriers (Blackburn *et al.* 2011) that would otherwise limit their spread, allowing them to impact ecosystems directly and indirectly (Ehrenfeld 2010; Fei *et al.* 2014; Ruesink 2018; Crystal-Ornelas and Lockwood 2020). These impacts include changes to vegetation communities (Peterson 1982; Summerson and Peterson 1984), geomorphology (Fei *et al.* 2014; Ruesink 2018), nutrient dynamics, carbon exchange cycles, and disturbance (Ehrenfeld 2010) and deposition regimes (Fonsesca *et al.* 1982; Peterson *et al.* 1984). The combination of some or all of these changes can result in a reduction of native biodiversity (D'Antonio & Vitousek 1992; Mack *et al.* 2000; Minchinton & Bertness 2003; Clavero and Garcia-Berthou 2005).

Phragmites australis subsp. *australis* (hereafter: *P. australis*) is an invasive macrophyte prevalent in tidal areas, roadside ditches, and wetlands across North America (Chambers *et al.* 1999; Saltonstall 2002). Ranked as the top priority invasive plant in Canada in 2005 (Catling and Mitrow 2005), *P. australis* has wreaked havoc on Canada's inland and coastal freshwater wetlands. Native to Europe, *P. australis* has dominated over its native counterpart *P. australis americanus* (Saltonstall, 2002, 2003; Meadows & Saltonstall 2007) and other wetland plants in many regions of North America (Chambers *et al.* 1999; Saltonstall 2002; Wilcox *et al.* 2003; Markle *et al.* 2018). The successful invasion of *P. australis* into North America's coastal wetlands has been tied to increased road density (Catling and Carbyn 2007; Jodoin *et al.* 2008; Christen and Matlack 2009), unique and variable reproductive strategies (including dispersal through both seed and rhizome fragments, local clonal spread, and seedling establishment) (Besitka 1996; Koppitz 1999; Pellegrin and Hauber 1999; Belzile *et al.* 2010; McCormick *et al.* 2010), and artificial water-level control in the Laurentian Great Lakes and the coastal wetlands tied to them (Trexel-Kroll 2002; Wilcox 2004). A variety of taxa are affected by the invasion of *P. australis* into the Great Lakes coastal wetlands of Ontario, including the composition of marsh birds (Benoit and Askins 1999; Whyte *et al.* 2015; Robichaud and Rooney 2017), amphibians (COSEWIC 2010; Markle *et al.* 2018), reptiles (Hecnar and Hecnar 2010; Markle and Chow-Fraser 2018), fish (Warren *et al.* 2001; Croft-White *et al.* 2021), and invertebrates (Robichaud *et al.* 2021).

Point Pelee National Park (PPNP) is located along the northern shore of Lake Erie and is home to one of the largest remaining Great Lakes Coastal wetlands in Canada. Over 70% of the park is comprised of

wetland habitat (Parks Canada 2010) which supports very high numbers of species at risk (Bortoluzzi 2019) and as such, is recognized as a Wetland of International Significance by UNSECO (Parks Canada Agency 2016). Unfortunately, *P. australis* has invaded and now dominates many areas of the wetland at PPNP (Markle et al. 2018). Markle et al. (2018) found that within the past two decades the number of *P. australis* stands increased from only four to 166 individual stands with a density of 11 stands per 100 hectares. As a result of this finding, PPNP is working towards a conservation plan for the marsh which includes discussion on the need for a management plan to target the spread of *P. australis*. Experimental treatment of *P. australis*-removal was to take place over water, but at the time of this project Glyphosate herbicide spraying over water had not been approved in Canada (Health Canada PCP 2002) nor in Canadian National Parks. Therefore, PPNP undertook the manual cutting of *P. australis* stems below the water level.

The goal of our study was to explore the changes in coastal wetland vegetation and invertebrate communities after manual *P. australis* removal. We sought to test whether removing *P. australis* would lead to local species richness that reflected nearby non-invaded wetlands. We did this by comparing vegetation and invertebrate communities between three wetland types: 1) a wetland currently invaded by *P. australis* (referred to as Invaded), 2) a wetland treated for *P. australis* invasion (referred to as Treated), and 3) a wetland that has never been invaded by *P. australis* (referred to as Non-Invaded). We hypothesized that if *P. australis* formed dense monocultural stands that limited light penetration and reduced growing capacity for other aquatic vegetation, then removing *P. australis* would lead to an increase in aquatic vegetation growth among other species. Specifically, we predicted that indicators of primary succession (including aquatic vegetation and emerging aquatic invertebrate communities) would be higher in abundance and greater in diversity within the Treated and Non-Invaded sites, and lower in the Invaded site.

Methods

Point Pelee National Park

PPNP is a 15-km² national park in Ontario, Canada along the shore of Lake Erie. *P. australis* was first noted in the park in 2000, though many believe it to have been present long before first identification. Over 90% of the *P. australis* distribution has displaced pre-existing natural marsh habitats, and open water habitat has decreased by 10% since 1959, with many small and non-connected pools of water having been infilled (Markle et al. 2018). Manual and mechanical removal of five hectares of *P. australis* was proposed to support the overall goal of restoring biodiversity and open water and edge habitat within the marsh (Parks Canada 2020). Successful removal of 9653.61 m² of *P. australis* occurred in 2020 near the southern-most extent of the Point Pelee marsh, followed by the burning of removed stems. An undisturbed *P. australis*-Invaded site (yellow) is located 500 m north of the Treated site (blue), and a Non-Invaded site (purple) is located 150 m south of the Treated site (Fig. 1).

Data Collection

Vegetation Collection

Vegetation data collection occurred between 7 July 2022 and 28 July 2022, at Point Pelee National Park. Vegetation data was sampled systematically using a 10-m x 10-m grid overlay across all three wetland sites (*P. australis*-Invaded, *P. australis*-Treated, Non-Invaded). We collected vegetation data at every grid intersection using a 1-meter x 1-meter sampling quadrat. We sampled 65 vegetation plots from the Treated site, 35 vegetation plots from the Invaded site, and 45 vegetation plots from the Non-Invaded site. Vegetation data included live species identification, percent cover of each live species (recorded as abundance), and live and dead stem count of *P. australis*.

Invertebrate Collection

Beginning 7 July 2022, four emerging aquatic invertebrate traps (EAIT) were randomly deployed in each site. EAITs are designed to capture all emerging aquatic invertebrates to allow for an estimate of invertebrate biomass/m². Due to field constraints, EAITs were altered to be 50 cm² for ease of travel through the marsh. EAITs are tent-like in structure with 500-um mesh netting (Anderson and David 2013, Figure S1) that leads to a 500 ml capture vessel. 200 mL of 95% propylene glycol was used as the killing agent in each capture vessel (Thomas, 2008). Capture vessels were collected and replaced every three weeks and specimens were rinsed and stored in 70% ethanol upon return to the lab. All EAITs were removed from the field on 16 September 2022.

Laboratory Methods

Identification of the invertebrates to the species level was accomplished through DNA identification in partnership with NatureMetrics, a commercial DNA lab.

DNA Extraction. Samples stored in 90% ethanol were shipped to the Nature Metrics North American office in Guelph, Ontario. Ethanol was drained from all samples and samples were then dried overnight at 30°C. Lysis buffer (modified from Ivanova et al. 2006) was added directly to the dried samples without homogenization. The amount of lysis buffer was relative to the weight of the sample. Samples were incubated at 56°C for approximately 3 hours with periodical mixing. An aliquot of the lysate was processed using DNeasy Blood and Tissue Kit (Qiagen) according to the manufacturer's protocols. An extraction blank (made of lysis buffer) was processed with each batch of samples as a negative control.

PCR Amplification. Replicate PCRs for each sample and extraction blank were amplified via a two-step PCR process, with tails added to the 5' end of taxon-specific primers which complements downstream adapter and index primer sequences. DNA was amplified in the first round PCR with modified mICOIntF & jgHCO2198 primers containing Illumina adapters (Wangensteen et al. 2018), which targets the Folmer region of the mitochondrial CO1 (cytochrome C oxidase subunit 1) gene. This region of the gene was targeted because it enables species identification across eukaryotes, including invertebrates (Hebert et. al. 2003). Positive and negative controls, consisting of proprietary synthetic sequences (that do not match

known biological records) and PCR-grade water, respectively, were included with every PCR plate to verify amplification performance. PCR amplification success was confirmed visually by gel electrophoresis.

Library Preparation and Sequencing

Because the invertebrate bulk tissue samples were of high quality and quantity, all PCR replicates were successful. First round PCR replicates were pooled per sample and purified using magnetic beads. A sequencing library was prepared from the purified amplicons using unique dual indexes (minimizing crosstalk), following Illumina's 16S Metagenomic Sequencing Library Preparation protocol (16s-metagenomic-library-prep-guide-15044223-b.pdf). Indexed PCR products were subsequently purified using magnetic beads prior to being quantified, normalised, and pooled in equal volumes. The final pooled library was denatured, diluted and sequenced on an Illumina MiSeq using a V3 600 cycle reagent kit. A PhiX control library was included on the sequencing run to provide a quality control for cluster generation, sequencing, and alignment, and a calibration control for cross-talk matrix generation, phasing, and pre-phasing.

Bioinformatic Methods. Sequences were demultiplexed (separated to corresponding samples) using bcl2fastq and subsequently processed to obtain Amplicon Sequence Variants (ASV), which are any one of the inferred single DNA sequences obtained from metabarcoding processes. Paired-end FASTQ reads for each sample were merged with USEARCH (Edgar, 2010). Forward and reverse primers were trimmed from the merged sequences using cutadapt (Martin, 2011) and a length filter applied. These sequences were quality filtered with USEARCH to retain only those with an expected error rate per base of 0.05 or below and dereplicated by sample, retaining singletons. Unique sequences from samples were denoised in a single analysis with UNOISE. Taxonomic assignments were made via sequence similarity (blastn; (Altschul et al., 1990; Camacho et al., 2009) searches of the ASV sequences against reference databases appropriate for the assay. Hits were required to have a minimum e-score of 1e-20 and cover at least 90% of the query sequence. The taxonomy associated with each hit was converted to the GBIF taxonomic backbone to allow blastn results from curated databases (including BOLD & NCBI nt database) to be comparable for the following step. NatureMetrics uses proprietary methods to curate and filter out database errors through whitelisting, blacklisting, and human curation based on country lookups to ensure that there is reasonable support that the sequence has been correctly associated in the database. Assignments were made to the lowest possible taxonomic level where there is consistency in the matches. ASVs were then clustered at 97% similarity with USEARCH to obtain OTUs (Operational Taxonomic Unit).

Family level identification was used in analysis as there are no significant differences in the results of descriptive statistical analysis when using Genus or Family level ID (Pires et al. 2021).

Data Analysis

Vegetation and emerging aquatic invertebrate species with two or fewer occurrences within the entire dataset were removed (n = 5 vegetation species removed, n = 28 invertebrate families removed, Table S1). This was done to reduce the impact of rare species on distance-based community composition analysis.

Vegetation Analysis. We tested for the effect of wetland type using general linear models to compare taxonomic richness, abundance (measured as percent cover of each live species within the vegetation plot), total *P. australis* stem density/m², and Shannon Weiner diversity index (H) as response variables with wetland type as the fixed factor. If wetland type was significant, we performed a Tukey's post hoc test. General linear modelling was performed using *lm* (R Core Team 2021) and *agricolae* (de Mendiburu 2020) in R v. 4.2.2 (R Core Team 2021).

To determine if the vegetation community composition differed among sites, we performed an Analysis of Similarity (ANOSIM) using the Bray-Curtis dissimilarity index. ANOSIM uses a ranked dissimilarity matrix to determine the degree of separation between the groups of study (in our case, the three wetland types). Test R statistics are between 0 and 1, with values $\cong 1$ representing the replicates within the group being more similar to each other than they are to the other groups, while values $\cong 0$ implies little to no difference in replicate structure between groups (Clarke and Warwick 2001). We used the Bray-Curtis matrix because it considers both species presence/absence and abundance. To compliment the ANOSIM analysis, we used a perMANOVA test and conducted a non-metric multidimensional scaling (NMDS) ordination. NMDS allowed us to visualize the differences in vegetation community among the three wetland patches. Additional site characteristics (including percent of open water and percent of dead cover) were included within the NMDS to help explain patterns in vegetation community structure.

Emerging Aquatic Invertebrate Analysis. Emerging aquatic invertebrate data did not meet the assumptions of normality and therefore we used permutational general linear models to compare taxonomic richness, total density/m², and Shannon Weiner diversity index (H) as response variables with wetland patch as the fixed factor. If wetland patch was significant, we performed a Tukey's post hoc test. Permutational general linear modelling was performed using *lmPerm* (Wheeler & Torchiano 2016) and *agricolae* (de Mendiburu 2020) in R v. 4.2.2 (R Core Team 2021).

We conducted a very similar set of statistical tests when analyzing the emerging aquatic invertebrate (EAI) data. We used an Analysis of Similarities (ANOSIM) with Bray Curtis index to determine if there is a statistically significant difference in emerging aquatic invertebrate communities among the three wetland patches. Following this, we paired a perMANOVA test with a non-metric multidimensional scaling (NMDS) ordination to visualize the differences in EAI community among the wetlands. Both sets of analysis involving ANOSIM and NMDS were performed using the *vegan* package (Oksanen et al. 2020) in R v. 4.2.2 (R Core Team 2021). All figures were created with *ggplot* (Whickham 2016).

Results

Vegetation

A total of 14 emerging plant species were detected: seven within the Invaded patch, 14 within the Treated patch, and 12 within the Non-Invaded patch. General linear models paired with analysis of variance (ANOVA) revealed that coastal wetland vegetation richness was significantly higher ($F_{2,148} = 20.785$, $p =$

1.108E-08) in the Treated patch (mean = 4.29 species / plot) and the Invaded patch (mean = 4.0 species/plot) compared to the Non-Invaded patch (mean = 2.28 species/plot; Fig. 2). Plant species abundance (excluding *P. australis*; measured as percent cover) was significantly higher ($F_{2,147} = 59.948$, $p = 2.2E-16$) in the Treated (mean = 93.2% coverage) and Non-Invaded patch (mean = 95.76% coverage) than the Invaded wetland patch (mean = 53.28% coverage) (Fig. 2). As well, total *P. australis* stem density (stems / m²) was significantly higher ($F_{2,147} = 149.925$, $p = 1.11E-16$) in the Invaded patch (mean = 72.56 stems / m²) than the Treated patch (mean = 4.77 stems / m²) or Non-Invaded patch (mean = 2.13 stems / m²) (Fig. 2). There was no significant difference in total *P. australis* stem density between the Treated and Non-Invaded patches. Among the three wetland patches, there was no significant difference detected in Shannon DI ($F_{2,147} = 0.6879$, $p = 0.5$).

The ANOSIM using Bray-Curtis dissimilarity matrix showed a significant difference in wetland composition between the Invaded and Non-Invaded wetlands ($R = 0.679$, $p = 0.001$), and showed significant similarity in wetland composition between the Treated and Non-Invaded wetlands ($R = 0.134$, $p = 0.001$). A moderate R test score of $R = 0.401$ ($p = 0.001$) was expressed when comparing wetland vegetation between Treated and Invaded wetlands.

The mean distance to the group centroid was 0.2521 in the Invaded wetland, 0.4124 in the Non-Invaded wetland and 0.4889 in the Treated wetland, indicating that the beta diversity of wetland vegetation was lowest in the Invaded wetland, and highest in the Treated wetland. There was a significant difference in the homogeneity of variances among the three wetlands (PERMDISP, $F_{2,148} = 24.328$, $p < 0.001$). Because wetland vegetation did differ in the homogeneity of variance among wetland patches, we interpret the statistically significant perMANOVA (pseudo- $F_{2,148} = 28.67$, $p < 0.001$, Figure S2) as indicating a difference in dispersion and location effects, where location effects refer to the effect on the mean abundance of some species, and dispersion effects refer to the effect on variability.

Our final NMDS ordination solution was three-dimensions with a final stress of 0.109, indicating a good fit. Final stress was repeated four times in 20 tries with a non-metric R^2 of 0.98 and a linear fit R^2 of 0.92. There was no overlap of the Invaded and Non-Invaded wetlands along axis 1 (Fig. 3). The Treated and Non-Invaded wetlands overlap on both axis 1 and 2 (Fig. 3). There was less variation in the Invaded plots, and they were uniquely characterized by high densities of *P. australis*, *H. ranae* (European frogbit; invasive), and dead cover (Fig. 3). Prominent features of both the Treated and Non-Invaded patches included high densities of *C. occidentalis* (button bush; native), *Lemnoideae* spp. (duckweed; native), *Typha* spp. (cattail; a mixture of native, invasive, and their hybrids), *S. eurycarpum* (large fruited burred; native), *N. lutea* (yellow water lily; native), *B. frondose* (devil's beggar tick; native), and *D. loosestrife* (swamp loosestrife; native) (Fig. 3). On axis 1 and 3 there was significant overlap between the Treated and Non-Invaded patches with *H. ranae* (European frogbit), *C. occidentalis* (button bush), and *Lemnoideae* spp. as the featured vegetation (Fig. 3). Through the combination of perMANOVA results, ANOSIM results, and the final NMDS ordination, we determined there was a significant difference in community composition of emergent aquatic vegetation among wetland patches.

Emerging Aquatic Invertebrates

A total of 44 families were found: 27 families were detected in the Invaded patch, 34 within the Treated patch, and 38 within the Non-Invaded patch. Results of statistical analysis using permutational general linear models paired with analysis of variance (ANOVA) revealed that Great Lakes coastal wetland invertebrate density/m² was significantly higher ($F_{2,36} = 9.019$, $p = 0.0007$) in the Non-Invaded patch (mean = 825.67 / m²) than the Treated (mean = 502.67 / m²) or Invaded patch (291.33 / m²) (Fig. 4). Invertebrate species richness was significantly higher ($F_{2,36} = 10.397$, $p = 0.0003$) in the Non-Invaded patch (mean = 17.00/ EIT) and Treated patch (18.83 / EIT) than the Invaded patch (13.08 / EIT) (Fig. 4). As well, Shannon Diversity index was significantly higher ($F_{2,36} = 5.889$, $p = 0.006$) in the Treated patch (mean = 2.29) than the Non-Invaded patch (mean = 1.62) and the Invaded patch (mean = 1.71).

The ANOSIM test using Bray-Curtis dissimilarity matrix showed a significant difference among all three patches, with the greatest difference in invertebrate composition between the Invaded patch and Treated patch ($R = 0.992$, $p = 0.001$), followed by a difference (with slight overlap in composition) between the Non-Invaded patch and Treated patch ($R = 0.630$, $p = 0.001$). A moderate R test score of $R = 0.549$ ($p = 0.001$) was expressed when comparing wetland coastal invertebrate community between Non-Invaded and Invaded patch, representing a difference in invertebrate community composition, though some moderate overlap in composition does occur.

The mean distance to the group centroid was 0.4055 in the Invaded patch, 0.2364 in the Non-Invaded patch and 0.1581 in the Treated patch, indicating that the beta diversity of wetland emerging invertebrates was lowest in the Treated patch, and highest in the Invaded patch. There was a significant difference in the homogeneity of variances among the three patches (PERMDISP, $F_{2,35} = 24.18$ $p < 0.001$). Because invertebrate composition did differ in the homogeneity of variance among wetland patches, we interpret the statistically significant perMANOVA (pseudo- $F_{2,35} = 19.681$, $p < 0.001$; Figure S3) as indicating a difference in dispersion and location effects, where location effects refer to the effect on the mean abundance of some species, and dispersion effects refer to the effect on variability.

Our final NMDS ordination solution was two-dimensions with a final stress of 0.110, indicating a good fit. Final stress was repeated 4 times in 20 tries with a non-metric R^2 of 0.988 and a linear fit R^2 of 0.949. There is a very slight overlap of the Invaded patch and Treated patch along the 1st and 2nd axis of the NMDS plot (Fig. 5). The Non-Invaded patch overlaps with both the Treated and Invaded patch along axis 1 and 2 but is also characterized by high densities of invertebrate families that are absent from the other patches (Fig. 5). The Treated patch is characterized by high densities of *Dytiscidae* and *Limoniidae*; the Non-Invaded patch is characterized by very high densities of *Sciomyzidae*, *Chironimidae*, and *Staphylinidae*; the Invaded patch is characterized by the presence of *Scirtidae*, *Hesperiidae*, and *Coenagrionidae* (Fig. 5). The perMANOVA results combined with the ANOSIM and the final NMDS ordination describe a significant difference in community composition of emerging invertebrates among wetland patches.

Discussion

Our findings support our hypothesis that *P. australis* invasion and subsequent treatment would affect the aquatic emergent vegetation and emerging aquatic invertebrate community composition within the Great Lakes coastal wetlands at Point Pelee National Park. Vegetation species richness and abundance was significantly lower in the Invaded patch when compared to both the Treated and Non-Invaded patches. As well, vegetation community composition was significantly different between the Invaded patch and both the Treated and Non-Invaded patches. Total abundance and species richness of emerging aquatic invertebrates was highest in the Non-Invaded patch, and lowest in the Invaded patch and overall emerging invertebrate community composition was different among the three wetland patches. In general, measures of species richness in the Treated patch were closer to the Non-Invaded patch than the Invaded patch.

P. australis Response to Treatment

Manual cutting and burning of *P. australis* requires extensive physical labour and can be quite time consuming. Our results show that manual cutting and drowning of *P. australis* followed by the burning of cut stems is a sufficient method to remove *P. australis* at a small scale. Two years after *P. australis* removal including annual spot treated follow up, total stem density/m² averaged 4.77 stems within the Treated patch, and 72.56 stems within the Invaded patch.

Vegetation Community Composition

Vegetation species richness was higher in the Treated and Non-Invaded patches compared to the Invaded patch (Fig. 2), a finding that is common following the removal of invasive *P. australis* (Farnsworth and Meyerson 1999; Bonello and Judd 2020). Within two years of management, Farnsworth and Meyerson (1999) saw an increase in species richness that was not observed in the invaded sites within their study. Like our study, Farnsworth and Meyerson (1999) made no effort to encourage the growth of specific plants, therefore new growth of non-*P. australis* plants can be assumed to come from the rich seedbank that persevered despite previous *P. australis* invasion (van der Valk and Pederson 1989; Barrett 1994).

Two years after *P. australis* removal the vegetation community composition was very different when comparing the Invaded patch to both the Treated and Non-Invaded patches (Fig. 3); a trend that is not uncommon in the literature (Farnsworth and Meyerson 1999; Zimmerman et al. 2018; Bonello and Judd 2020; Robichaud and Rooney 2021). Like Bonello and Judd (2020), we observed high densities of *P. australis* at the Invaded sites in contrast to high densities of forbs and emergent aquatic plants in both the Treated and Non-Invaded sites (Fig. 3). Invaded plots were characterized by high coverage of *P. australis* (*P. australis australis*), European frogbit (*Hydrocharis morsus-ranae* L.), and duckweed (*Lemna minor* & *Lemna major*), while the Treated and Non-Invaded patches resembled a Buttonbush Mineral Deciduous Thicket Swamp (PPNP DIA Marsh Restoration 2021), characterized by the presence of buttonbush trees (*Cephalanthus occidentalis*), and other aquatic emergent plants (Fig. 3). A recent study looking at the removal of invasive *P. australis* at another Lake Erie coastal wetland saw an increase in

invasive *Hydrocharis morsusrae* (European frog-bit) following the removal of *P. australis* (Robichaud and Rooney 2021). Robichaud and Rooney (2021) observed *H. morsusrae* co-occurring with *P. australis* before treatment and reported an increase from 1.73% coverage to 48% coverage two years post *P. australis* removal. *H. morsusrae* is an invasive aquatic plant that is native to Europe, Africa, and Asia (Catling *et al.* 2003). While the literature surrounding *H. morsusrae* is not as comprehensive as that of *P. australis*, recent data suggest that it can have serious negative effects on native aquatic plant diversity (Catling *et al.* 1988; Zhu *et al.* 2018). Our study does not report on pre-treatment coverage of any aquatic plant, however two years-post treatment, *H. morsusrae* has an average cover of 26.96% in the Treated patches and 17.28% in the Invaded patches. Monitoring of *H. morsusrae* should continue to ensure it does not outcompete the desired regrowth of native aquatic plants. Despite of the current coverage of *H. morsusrae* within the three patches, our data shows that the overall vegetation community composition is different when comparing the Invaded site to both the Treated and Non-Invaded sites.

A common metric of measuring restoration success is to compare treated sites to remnant, non-invaded sites (Ruiz-Jaen and Aide 2005; Mathews and Spyreas 2010; McDonald *et al.* 2016); if the sites are similar in their composition, the restoration project might be considered successful. Two years-post *P. australis* removal, the vegetation community composition in our plots at Point Pelee National Park is similar between the Treated and Non-Invaded sites (Fig. 3). Vegetation plots of both sites take up similar ordination space visualized in the NMDS solution (Fig. 3) and reflect comparable vegetation communities. Zimmerman *et al.* (2018) found similar results after herbicide treatment within a freshwater tidal wetland in the Hudson River, though these results were specific to the smaller plots (0.04ha) within their study. At Point Pelee National Park, colonization of the Treated site was primarily advanced by native aquatic species. In addition to long-term spot treatment of *P. australis* re-growth (Smith 2005), the observed plant diversity of the Treated and Non-Invaded sites may lessen the chance of successful *P. australis* (re)invasion (Peter and Burdick 2010). Peter and Burdick (2010) found that interspecific competition of native plants reduced *P. australis* density, survival, and shoot length by 60%. When *P. australis* was planted in a plot with greater native plant diversity, *P. australis* growth and survival declined (Peter and Burdick 2010). We hope that the successful colonization of the Treated site with native aquatic vegetation will reduce the likelihood of future *P. australis* re-invasion at Point Pelee National Park.

Emerging Invertebrate Community Composition.

Our first goal in sampling invertebrates was to determine if the density and species richness of emerging invertebrates would differ among the Treated, Invaded, and Non-Invaded sites. We found that the Non-Invaded site supported the highest abundance of invertebrates with almost 3-fold more invertebrates/m² than the Invaded site. While the Treated site supported less invertebrates than the Non-Invaded site, it did support almost 2-fold more invertebrates/m² than the Invaded site. Schummer *et al.* (2012) found similar results after comparing total aquatic macroinvertebrate abundance between a treated and *P. australis*-invaded wetland along Lake Erie. In three northern Great Lakes coastal wetlands, Lawrence *et al.* (2016) found higher macroinvertebrate densities and biomass in native zones compared to zones of invasive *Typha x glauca*; a macrophyte similar to *P. australis* in stem density growth and habitat homogenization.

Not only was abundance/m² higher in the Non-Invaded and Treated site compared to the Invaded sites at PPNP, so too was species richness. On average we saw 5–6 more invertebrate families present in traps from the Treated and Non-Invaded sites than traps from the Invaded site. The results reported here show some consistencies with other studies reporting on the effect of *P. australis* removal in Great Lake coastal wetlands; two years post *P. australis* removal along the shore of Lake Erie, Robichaud et al. (2021) reported higher invertebrate densities in herbicide-treated versus invaded wetlands and higher taxonomic richness in remnant wetlands than treated wetlands. However, Robichaud et al. (2021) also reported lower invertebrate densities in the non-invaded wetlands compared to the herbicide-treated wetlands and higher taxonomic richness in the invaded wetlands than herbicide-treated wetlands, which is contradictory to our findings. Along the southern shores of Lake Erie following *P. australis* treatment, benthic invertebrate diversity increased with *P. australis* cover (Holomuzki and Klarer 2010), and overall densities were similar between invaded and non-invaded wetlands (Kulesza et al. 2008; Holomuzki and Klarer 2010; Robichaud et al. 2021). We should note that herbicide was used to treat *P. australis* invasion at both sites of interest in the studies above (Kulesza et al. 2008; Robichaud et al. 2021). Invertebrate detritivores may be attracted to the large amount of left-over litter following herbicide treatment as this may act as suitable breeding and foraging habitat. At Point Pelee National Park, *P. australis* was removed from the wetland and burned in piles, negating the opportunity for an influx of invertebrate detritivores. An influx of nutrients is released from disturbed soils during the restoration process which may create habitat conducive to invertebrate recolonization (LaGrange and Dinsmore 1989; McKee and Baldwin 2000; Gleason et al. 2004). As well, the Non-Invaded and Treated patches at PPNP support diverse vegetation community structure which may support higher densities of macroinvertebrates by providing habitat, refugia, and food sources (Angradi et al. 2001). Future research should look at the effect of different *P. australis* treatment methods on invertebrate densities and taxonomic richness.

Our second goal in sampling invertebrates was to examine the emerging invertebrate communities and determine if they differed among or between sites. We found that the invertebrate community composition was quite different between the Treated and Invaded sites, as observed from very little overlap on the NMDS ordination (Fig. 5) and a very high ANOSIM R² output. The Treated site was characterized by high densities of *Dytiscidae*, commonly known as predacious diving beetles. *Dytiscidae* preferentially choose shallow vegetation habitat such as swamps and marshes and often lay their eggs in or on vegetation at the water's surface (Thorp and Covich 2001). *Dytiscidae* are best suited to the vegetation composition described above within the Treated and Non-Invaded sites, as evidenced by the lack of floating plant life within the Invaded site. The Invaded site was characterized by relatively high densities of *Scirtidae*, commonly known as marsh beetles. *Scirtidae* are detritivores (Thorp and Covich 2001) and their increased abundance within the Invaded site could relate to the increase in dead cover seen within Invaded vegetation plots (Warren et al. 2001) (Fig. 3). The Non-Invaded site was characterized by *Sciomyzidae* ("marsh fly"), *Delphacidae*, and *Chironomidae* ("midge"). Robichaud et al. (2021) also reported very high densities of *Chironomidae* within their study, however these densities were most evident within the herbicide-treated wetlands. *Chironomidae* are a relatively tolerant family of

Diptera and, despite having significant densities within the Non-Invaded site, were still present in the Treated and Invaded sites.

There has been very little research studying the differences in emerging invertebrate community composition among *P. australis*-treated, invaded, and non-invaded habitat, with even less focussing on Great Lakes coastal wetlands. One study of note took place along the coast of Lake Erie at Long Point Provincial Park. Robichaud et al. (2021) reported that herbicide-treated wetlands had a very different invertebrate composition than both invaded and remnant wetlands, however the remnant wetlands within their study were highly invaded by *Typha x glauca* and did not necessarily represent pristine Great Lake coastal wetland habitat. Leonard *et al.* (2021) reported that invertebrate community structure was significantly different between *P. australis*-invaded sites and native *Salicornia rubra*-dominated sites in a saltwater wetland at Great Salt Lake in Utah, USA. However, the invertebrate composition was similar between *P. australis*-invaded sites and two other key habitats, *Schoenoplectus acutus*- and *Bolboschoenus maritimus*-dominated sites. We surmise that emerging invertebrate composition results are highly dependant on the structure of the wetlands, especially when additional invasive and non-invasive macrophyte species are present in non-invaded wetlands (Whyte et al. 2009)

Impacts of *P. australis* Invasion and Removal on Great Lakes Wildlife

We identified the vegetation and emerging aquatic invertebrate communities between the Treated, Invaded, and Non-Invaded patches at Point Pelee National Park because we considered these taxa to be good indicators of primary succession following restoration efforts. Across the entire Great Lakes basin, over 260 species, including waterfowl, breeding birds, herpetofauna, and fish species rely on the Great Lake coastal wetlands (Sierszen *et al.* 2012), and many of these species rely on healthy vegetation and invertebrate communities for survival. Reduced vegetation complexity has led to changes in fish (Hook *et al.* 2001; Leblanc *et al.* 2014), wetland bird (Meyer et al. 2010), and herpetofauna (Markle et al. 2018) composition within Great Lakes coastal wetlands. Aquatic emerging invertebrates are important food sources for fish (NOAA; Casselman and Lewis 1996), anurans, (Brown 1974) and birds (Richardson 1973; Newton 1998; Murkin and Batt 2012) within wetland systems and the reduced emerging invertebrate densities observed in the *P. australis*-Invaded site could negatively affect wildlife species (e.g., Kosteche *et al.* 2005). While many waterfowl and shorebird species are invertebrate generalists (Cavitt 2008), an overall reduction in invertebrate abundance may cause declines in bird population sizes and survival rates (Kosteche *et al.* 2005). Likewise, Markle et al.'s (2018) update of the invasion status of *P. australis* and *Typha x glauca* at Point Pelee National Park coincided with the decline in a variety of herpetofauna species. The interaction between *P. australis* invasion and reduced invertebrate density may be a contributing factor to the reported decline of herpetofauna diversity at Point Pelee National Park, though a directed study is needed to confirm this hypothesis. By removing *P. australis* from the wetlands at Point Pelee National Park, we have seen an increase in vegetation and invertebrate density, richness, and complexity that should result in the increased support of wetland taxa.

Conclusion

Point Pelee National Park is home to one of the largest remaining Great Lakes coastal wetlands in Canada. Two years after the successful manual removal of *P. australis* subsp. *australis*, native vegetation and emerging aquatic invertebrate richness and density was higher in the Treated site compared to the Invaded site. Community composition of the vegetation and emerging invertebrates were significantly different between the Treated and Invaded sites, and the vegetation composition within the Treated site resembled the vegetation composition of the Non-Invaded site. Despite the long-term management required to fully eradicate *P. australis* from Point Pelee National Park, our findings suggest it is possible to gradually return to native coastal wetland biodiversity.

Declarations

Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors have contributed to the manuscript and agreed with its contents. We look forward to your review. All authors contributed to the study conception and design. Material preparation and data collection were performed by Meghan Ward, Jeff Bowman and Tara Degazio. All analysis were performed by Meghan Ward. The first draft of the manuscript was written by Meghan Ward and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures



Figure 1

Point Pelee National Park is located along the eastern shore of Lake Erie in Ontario, Canada. The wetlands sites within this study are identified above: Invaded site (yellow circle, top), Treated site (blue square, middle), Non-Invaded site (purple triangle, bottom)

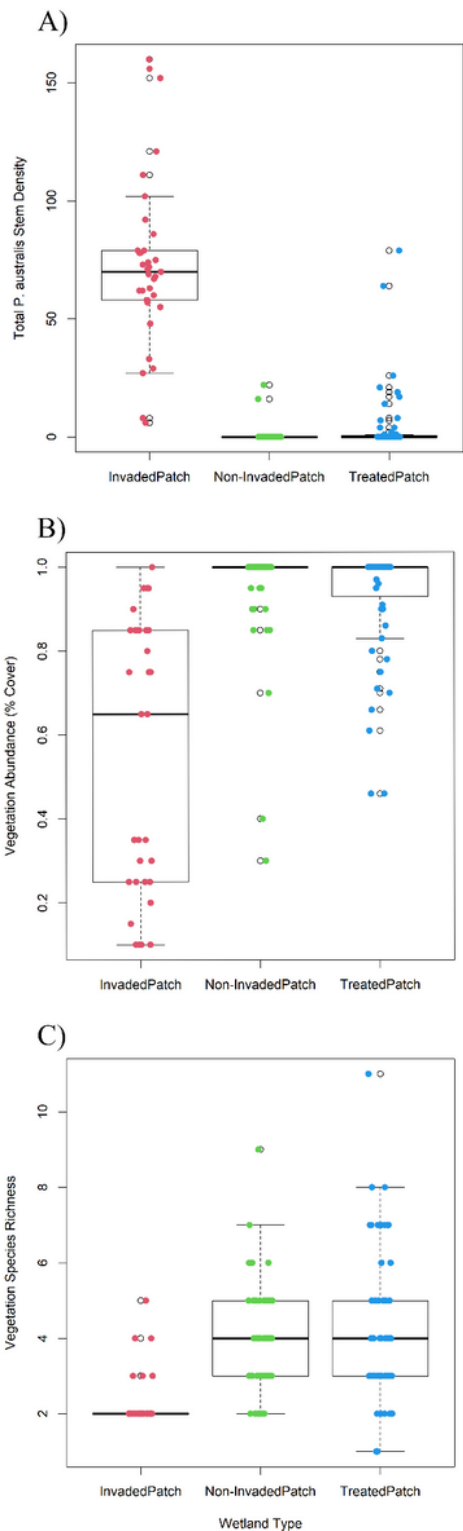


Figure 2

P. australis stem density (A), vegetation abundance (B), and vegetation species richness (C) between three wetland patches at Point Pelee National Park. Vegetation species richness was highest within the Treated patch, and significantly lower within the Invaded patch. Mean abundance (measured as percent cover) of non-*P. australis* plants was higher in the Treated and Non-Invaded patches. *P. australis* stem density varied between the three wetland patches; highest density occurred in the Invaded patch and lowest density was observed in the Non-Invaded patch

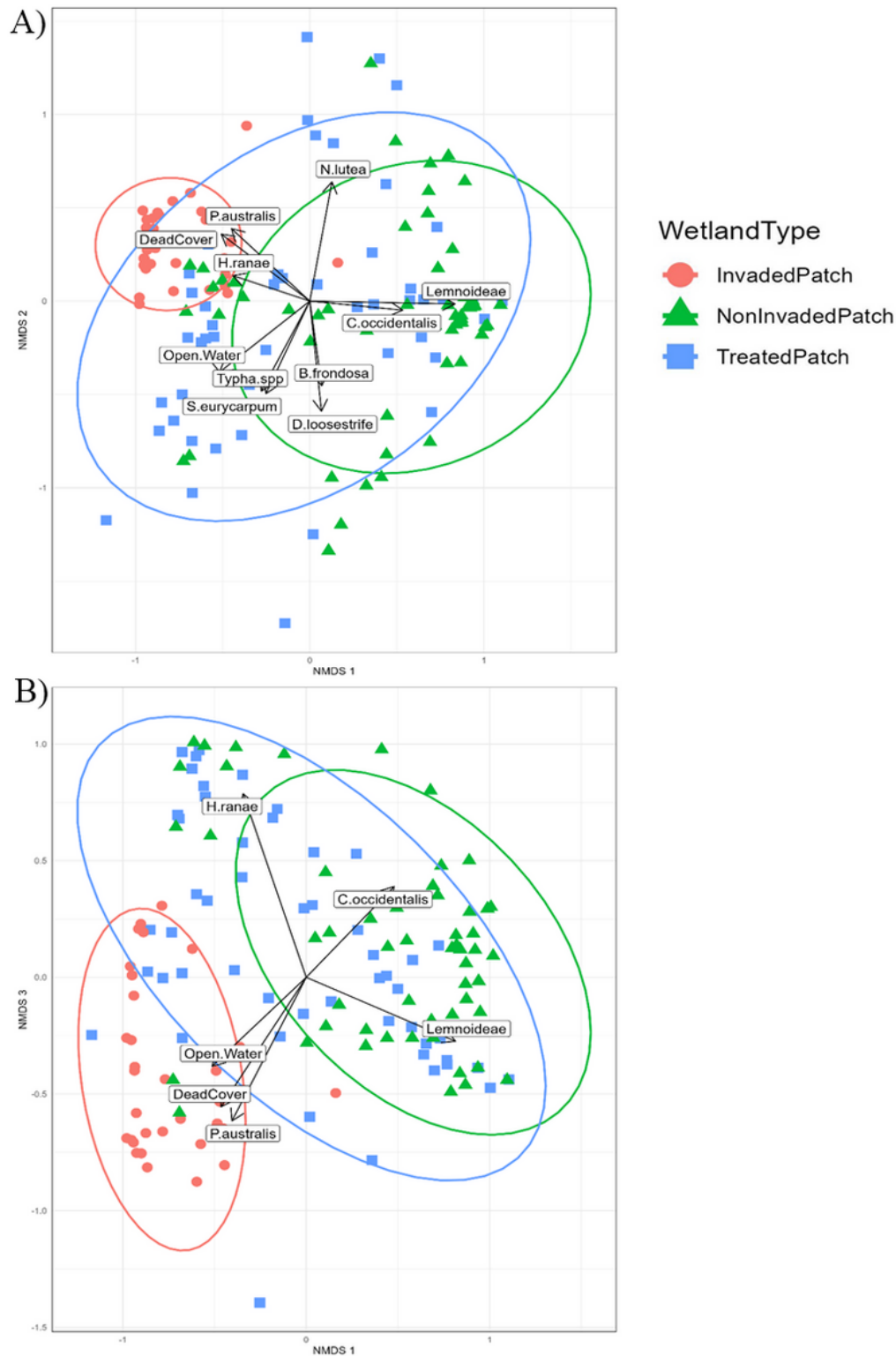


Figure 3

NMDS ordination solution, using Bray-Curtis dissimilarity matrix, of emergent coastal wetland vegetation with correlated environmental characteristics. 90% CI ellipses identify three wetland patches of interest. 'DeadCover' refers to standing dead *P. australis* stems.

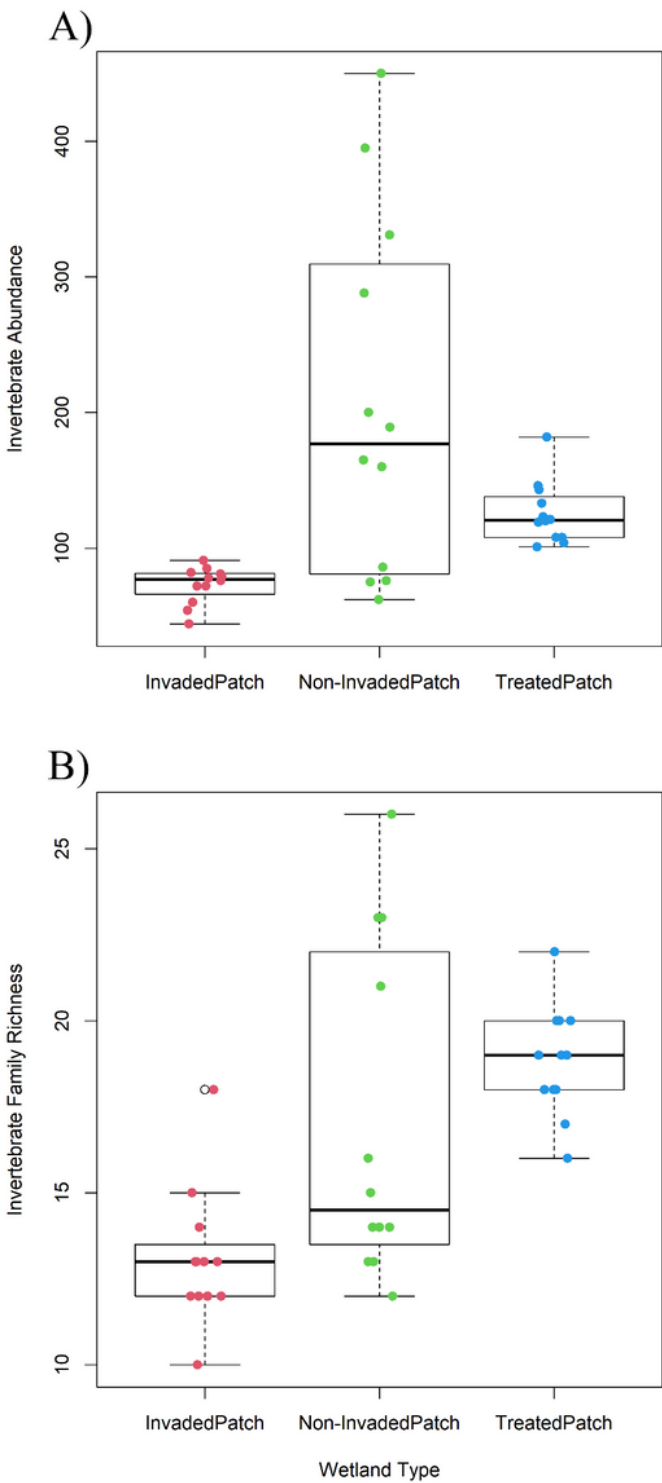


Figure 4

Compares invertebrate abundance (A) and species richness (B) between three wetland patches at Point Pelee National Park. Mean invertebrate species richness was highest Treated patch and lowest in the Invaded patch. Mean invertebrate abundance was highest in the Non-Invaded patch and lowest in the Invaded patch.

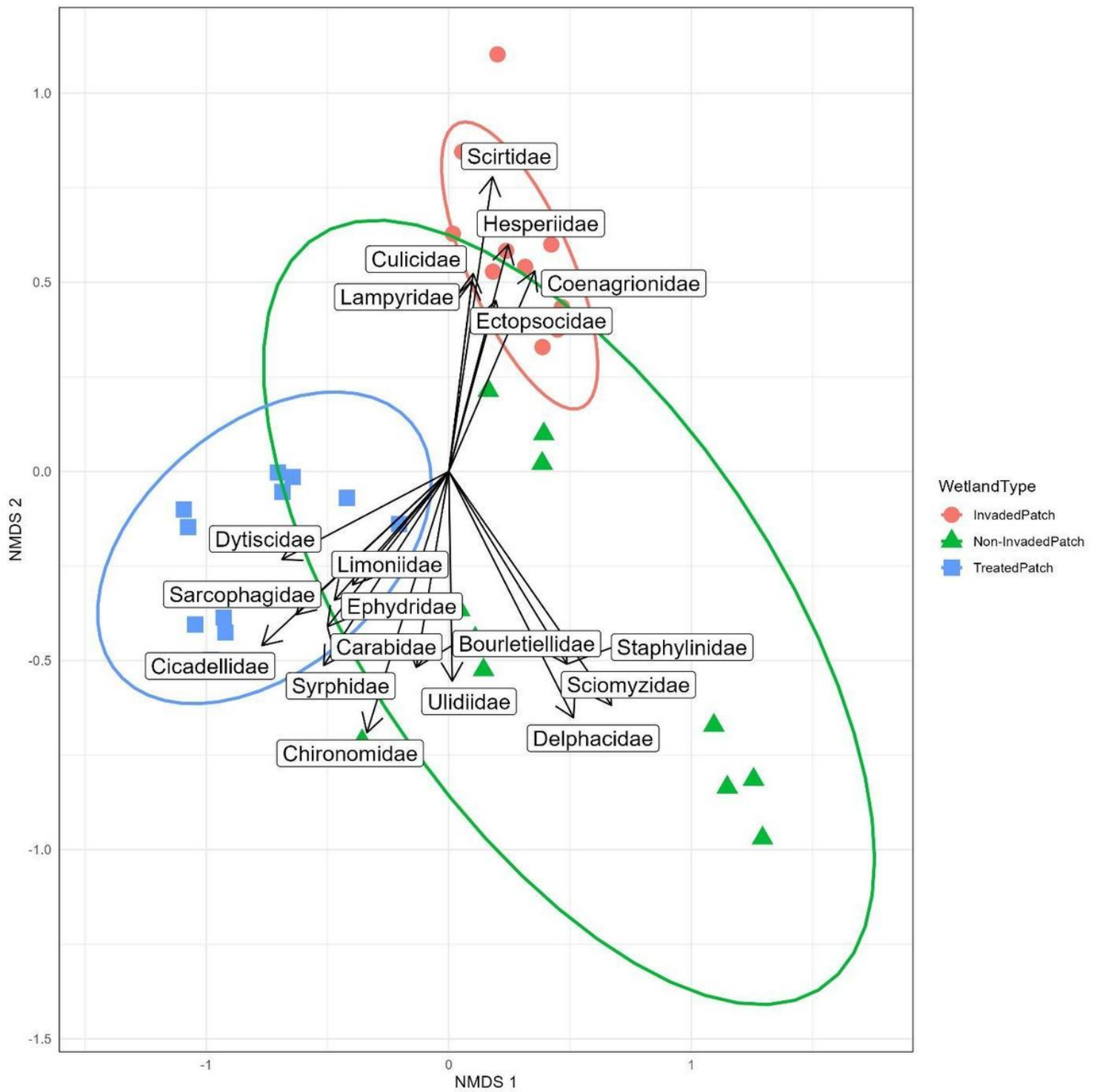


Figure 5

NMDS ordination solution, using Bray-Curtis dissimilarity matrix, of emerging aquatic invertebrates collected from Point Pelee National Park from July – September 2022. 90% CI ellipses identify three wetland patches of interest.

Supplementary Files

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