Differences in above-ground resource acquisition and niche overlap between a model invader (*Phragmites australis*) and resident plant species: Measuring the role of fitness and niche differences in the field

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Abstract

Identifying the mechanisms that result in a “high impact” invasive species can be difficult. Coexistence theory suggests that detrimental invasive species can be better predicted by incorporating both niche differences and fitness differences than examining niche overlap alone. Specifically, detrimental invasive species should take up shared limited resources more efficiently than their neighbouring resident species. While there is clear evidence that invasive *Phragmites australis* is successfully displacing resident species, there remains few field studies that attempt to quantify the niche overlap and fitness difference between *P. australis* and the species it is displacing in the field. Using *P. australis* we measured differences in photosynthetic performance (carbon assimilation rates, $\delta^{13}\text{C}$, photosynthetic water use efficiency, biomass), the effects of competition for photosynthetically active radiation, and niche overlap between *P. australis* and three resident freshwater wetland species (*Calamagrostis canadensis*, *Carex aquatilis*, and *Typha* spp.) growing with or without interspecific competition. Invasive *P. australis* intercepted more photosynthetically active radiation, assimilated more carbon more efficiently, and had a larger niche region compared to resident species. Resident plant species showed a significant decrease in photosynthetic performance when growing in competition with *P. australis* and had a high probability of overlap onto the niche space of *P. australis*. These results provide evidence that the ability of *P. australis* to reduce the availability of a required resource and more efficiently use it over the growing season, while exhibiting high niche overlap with resident species, likely contributes directly to its success in North American freshwater wetlands.

Introduction

Identifying the mechanisms that confer an advantage to an introduced species can be challenging. Work rooted in niche theory suggests that a resident community may have niche space, or untapped resources, that can be exploited by an introduced species (e.g., Elton 1958; Richardson and Pyšek 2006). It is also often posited that a successful invader is a superior competitor compared to its native neighbours, though this advantage can be transient or might work in concert with other environmental variables (Gioria and Osborne 2014). For example, the interactions between environmental and biological components of a system will influence community composition and species establishment (e.g., Kraft et al. 2015), while fluctuations in spatial or temporal niche opportunities (e.g., Chesson and Huntly 1997) can favour the coexistence of seemingly similar species. The complexities of biological communities can make it difficult to predict the effects of invasive species using a unified framework.

Both community assembly (Pearson et al. 2018) and coexistence theory (e.g., Chesson 2000) have provided structures to guide invasion ecology that account for the complexities of biological interactions. In the community assembly framework, invasive species might “break the rules” of the resident community by having rare traits that benefit them relative to community-specific conditions (Pearson et al. 2018). This can include traits that allow them to better take up resources or cope with limited resources (Gioria and Osborne 2014). MacDougall et al. (2009) applied a coexistence theory framework to invasion ecology and proposed that niche differences (or differences that benefit a species when they are rare) and fitness differences (or differences that benefit one species regardless of their rarity in the community), jointly explain how introduced species become established and why they are deleterious to the resident community. Essentially, an introduced species with a large fitness difference and high niche overlap with the resident community is more efficient at drawing down shared resources and therefore more likely to establish and result in negative ecological effects on resident species (MacDougall et al. 2009).

Phragmites australis subsp. *australis* (European common reed) is a perennial wetland grass originally from Europe that is now found throughout North American wetlands (Saltonstall 2002). Compared to the North American native *Phragmites australis* subsp. *americanus*, invasive *P. australis* generates more above-ground biomass, and has a higher specific leaf area and relative growth rate (Mozdzer and Megonigal 2012). Additionally, invasive *P. australis* tolerates a wide range of environmental conditions. These include surviving in water depths ranging from 30 cm below to 70 cm above the ground-level (Haslam 1971), in salinities ranging from freshwater to salt marshes (e.g., Konisky and Burdick 2004; Vasquez et al. 2005), and in a wide range of soil nutrient concentrations (Packer et al. 2017) – for example, Meyerson et al. (1999) reported *P. australis* growing in soil with a range of 0.35–14.7 mg g⁻¹ nitrogen. Invasive *P. australis* also responds positively to disturbance and nutrient addition by increasing the density and height of above-ground shoots (Minchinton and Bertness 2003) and generates more biomass when grown in elevated CO₂ treatments, suggesting it may fare better under climate change (Mozdzer and Megonigal 2012). Due to the extensive amount of research conducted on invasive *P. australis*, it has been formally suggested as a model organism with which to study plant invasions (Meyerson et al. 2016).

Although challenging to work with because of its rhizomatous, perennial life history, invasive *P. australis* is interesting because of its ability to establish itself in highly productive wetland ecosystems where niche space should be scarce (e.g., MacArthur and Levins 1967; Levine and D’Antonio 1999; Keane and Crawley 2002). In saltmarshes (e.g., Chambers et al. 1999) and freshwater marshes (e.g., Wilcox 2012) of North America, invasive *P. australis* has replaced native vegetation communities and reduced plant species richness (Meyerson et al. 2000). The species-rich plant communities located in the coastal marshes of Long Point, a peninsula on the north shore of Lake Erie, are one such system that has been largely converted to invasive *P. australis* (haplotype M) in the last few decades (Wilcox et al. 2003). During this period of growth *P. australis* most often replaced emergent marsh, sedge meadows and meadow marsh (Wilcox et al. 2003; Jung et al. 2017). Emergent marsh was typically in deeper water (> 30 cm) and dominated by cattail; principally, *Typha x glauca* (Godr. (pro sp.)), an invasive cattail resulting from hybridization between *Typha latifolia* (L.) and *Typha angustifolia* (L.) (Pieper et al. 2020). On the opposite end of the moisture gradient (< 20 cm) was usually meadow marsh dominated by grasses (e.g., *Calamagrostis canadensis* ((Michx.) P. Beauv.)) and in between lay sedge meadow dominated by *Carex* spp.; mainly *C. aquatilis*). Remnant patches of these three marsh communities remain in Long Point, but recent work suggests that if water levels remain stable *P. australis* will continue to spread at current rates (14–37% annually), potentially eliminating these remnants of resident species (Jung et al. 2017).

We hypothesize 1) that *P. australis* more efficiently assimilates carbon than resident species, a fitness difference that contributes to its success in diverse vegetation communities, 2) that *P. australis* intercepts more photosynthetically active radiation than resident species, leading to a negative effect of competition for resident species, a niche difference that benefits *P. australis*, and 3) that *P. australis* exhibits considerable overlap with the niche space of key resident species that span a range in preferred water depths (*C. canadensis*, *C. aquatilis*, and *Typha* spp.) due to its wide range of environmental tolerances.

While there is clear evidence that *P. australis* is successfully displacing resident plant communities in freshwater marshes, no field studies have quantified niche overlap and fitness differences between *P. australis* and these key resident species. The marshes of Long Point thus provide an opportunity to test these hypotheses and the coexistence framework proposed by MacDougall et al. (2009) with a well-studied and problematic model invasive species (Meyerson et al. 2016). Thereby, we will explain a component of the mechanisms that make *P. australis* such a detrimental invasive species.

Methods

Study Site

We conducted our experiment in Long Point Provincial Park, Long Point, Ontario, CA (42°35'01" N, 80°22'37" W; Appendix A). Long Point is a freshwater coastal marsh located on the north shore of Lake Erie and is a designated World Biosphere Reserve, Ramsar Wetland, and a globally significant Important Bird Area. Wetland vegetation in these marshes assemble along a water depth gradient from deep standing water (up to 70 cm) to shallow standing water or saturated soils.

This range of water depths is subdivided into three distinctive vegetation communities: emergent marsh (deepest), sedge meadow (intermediate) and meadow marsh (shallowest). Each of these vegetation communities comprises multiple plant species, but evenness is typically low (Robichaud and Rooney 2021), with each community dominated by a characteristic rhizomatous perennial that reproduces sexually and asexually. Coincidentally, these are traits that are shared by *P. australis*. For emergent marsh, the dominant species is most likely *Typha x glauca*, but identification based on morphology is difficult in the field due to extensive hybridization (Travis et al. 2010; Bansal et al. 2019) so we instead refer to "*Typha* spp." throughout. Sedge meadow was most commonly dominated by *Carex aquatilis* (water sedge [Wahlenb.]) and meadow marsh by *Calamagrostis canadensis* (Canada bluejoint grass). Hereafter, *Typha* spp., *C. aquatilis*, and *C. canadensis* are referred to as "resident species." Like *P. australis*, *Typha x glauca* generates dense monocultures (e.g., Galatowitsch et al. 1999), and *C. canadensis* is taxonomically closely related to *P. australis* as they both belong to the Poaceae family.

Experimental set up

For our experiment we selected replicate phytometers (an individual stem/ramet used to measure plant responses to experimental manipulations) of *P. australis* and the three resident species representative of each remnant vegetation community. All phytometers were situated along the leading edge of a *P. australis* stand (Appendix A). This best approximates realistic competition in invaded areas, as *P. australis* relies mostly on clonal expansion once it has established itself through seeds or clonal propagules (Kettenring et al. 2016). To minimize intraspecific competition, we selected resident phytometers that were growing surrounded primarily by *P. australis* within the stand and *P. australis* phytometers that were growing surrounded by each resident species. All of the phytometers were established in the same area, with a maximum distance of 150 m between plots (Appendix A).

We selected 96 phytometers on 23-May-2016 (Appendix B) and 27-May-2017 (Appendix C), for a total of 192 phytometers. Each year, these included 24 phytometers of *Carex aquatilis* and 24 of *C. canadensis*. We included only 12 phytometers of *Typha* spp. each year as these were more robust and less prone to damage during the field season. We included 36 phytometers of *P. australis* (12 each to compare with the three resident species). Phytometer pairs of equivalent height were identified for each species and one member of each pair was assigned at random to the 'with interspecific aboveground competition' treatment while the other was assigned to the 'without interspecific aboveground competition' treatment. This ensured that both treatments included phytometers spanning the full range of early-growing season ramet heights (Appendix D).

To create the 'without interspecific aboveground competition' treatment, we clipped all plants growing in the 1 m² area surrounding the phytometer to within 2 cm of the soil. For the 'with interspecific aboveground competition' treatments, we did not alter the surrounding above-ground biomass within 1 m² around the phytometer. However, to limit potential clonal subsidy and standardize belowground interactions, as all the phytometer species are rhizomatous clonal species, we severed roots and rhizomes in both the 'with competition' and 'without competition' treatments by sawing the perimeter of the 1 m² plots to a depth of 50 cm with a hand saw. We performed this once, as pilot work determined that severing the below-ground material repeatedly caused physical disturbance detrimental to the phytometers.

Approximately every 10 days, we measured the height of phytometers and re-clipped the surrounding vegetation in the 'without competition' treatment. Over the course of the experiment all phytometers were subject to natural herbivory and physical stresses. Phytometers that were consumed or died are reported in Appendix B & C.

Once phytometers had matured (in July, but dates varied between years with interannual differences in weather), we measured the carbon assimilation rate ($\mu\text{mol CO}_2 \text{ s}^{-1} \text{ m}^{-2}$) (A) and photosynthetic water use efficiency ($\text{CO}_2 \text{ mmol s}^{-1} \text{ m}^{-2} \text{ H}_2\text{O}$) (WUE) of each phytometer using a CIRAS-3 true differential gas analyzer with a PLC3 Universal LED Light Unit (RGBW) and PLC3 narrow leaf cuvette (PP Systems, Amesbury, MA, USA). We selected a fresh, entire (e.g., no damage) leaf growing with maximum sun exposure from each phytometer and then measured a photosynthesis-irradiance (PI) curve in the field. The PI curve began by exposing the leaf to 1500 $\mu\text{mol s}^{-1} \text{ m}^{-2}$ of photosynthetically active radiation, equivalent to an average full-sunlight day during the growing season, and slowly reduced PAR to 1000, 500, 200, 100, 50, and 0 $\mu\text{mol s}^{-1} \text{ m}^{-2}$ while simultaneously measuring carbon assimilation and photosynthetic water use efficiency. Measurements at each PAR level were taken until carbon assimilation rates plateaued, which typically occurred within two to three minutes. We took these measurements from July 26th to August 2nd in 2016 and from July 4th to July 14th in 2017, with phytometers of the same species measured on the same day to reduce potential temporal differences in performance between treatments. We also measured the amount of PAR reaching the top of each phytometer relative to the incident PAR above the canopy using a LI-1500 Light Sensor Logger coupled with two LI-190R quantum sensors (Li-Cor Biosciences, Lincoln, NE, USA). These sensors were deployed to take simultaneous readings from above the canopy and at the top of the phytometer to most accurately calculate the percent of incoming PAR intercepted by the canopy. PAR measurements were taken on cloudless days, between 09:00 and 15:00 h.

To compare a proportion of the aboveground biomass produced by each species over the growing season, we clipped each phytometer at the base of the stem right before peak aboveground biomass occurred in early August of 2016 and mid-July of 2017. Research in these marshes determined that peak biomass for emergent marsh, meadow marsh, and *P. australis* vegetation communities occurred in mid-August 2016 and late July 2017 (Yuckin and Rooney 2019). Due to clonal origin of the phytometers and the extent of interweaving of roots and rhizomes within the upper 40 cm of sediment (Lei et al. 2019), below-ground biomass could not be accurately determined.

Resource Measurements

To characterize niche overlap among species, we collected environmental variables from sites dominated by each of the phytometer species: *P. australis* (n = 15), *Typha* spp. (n = 15), *C. aquatilis* (n = 15) and *C. canadensis* (n = 15) for a total of 60 sites. For resident species, we selected patches of remnant vegetation at equivalent water depths but not experiencing direct interactions with *P. australis* to best approximate their realized niche within the marsh. Sites for each species were a minimum of 10 meters from one another, and all of the sites were situated within 1000 m of the phytometers (Appendix A). At each site we collected a 10 cm deep soil core to measure soil nutrients, measured soil moisture using a WET sensor kit and HH2 moisture meter (Delta-T Devices, Burlington, ON), and measured the percent of incident PAR intercepted by the canopy by deploying the Li-Cor sensors to take simultaneous readings from the top of the canopy and the soil or water surface on cloudless days between 09:00 and 15:00 h.

Laboratory Analyses

Each phytometer was dried at 80°C for 24 hours and then weighed on an analytical balance to the nearest 0.0001 g to determine the aboveground biomass. For a subset of 48 phytometers from the 2016 season: ten individuals of each of the resident species (5 'with competition,' and 5 'without competition') (10 x 3 = 30 samples), and six *P. australis* phytometers (3 'with competition,' 3 'without competition') for each of the neighbouring species (6 x 3 = 18 samples), we also measured the carbon (% dry weight) and nitrogen (% dry weight) content from selected leaves. To relate these nutrient content measures to photosynthetic performance (e.g., Hirose and Werger 1987; Hirtreiter and Potts 2012), we also measured the $\delta^{13}\text{C}$ isotopic composition of each selected leaf. The plants in our study are all C_3 photosynthesizers which have $\delta^{13}\text{C}$ values that range between -20 to -37‰ (Kohn 2010). The C_3 photosynthetic pathway discriminates against the heavier ^{13}C isotope during stomatal diffusion and carboxylation by Rubisco (Fry 1992) - plants that discriminate less between C isotopes typically photosynthesize more efficiently and have a higher (less negative) $\delta^{13}\text{C}$ value (Farquhar et al. 1989; McAlpine et al. 2008).

Selected leaves were ground into a homogenous powder and a subsample of 1 mg collected for analysis of C, N and $\delta^{13}\text{C}$ by the Environmental Isotope Laboratory at the University of Waterloo. First, samples underwent combustion conversion to gas through a 1108 Elemental Analyzer (Fisons Instruments) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer. The %N and %C element content is a bulk measurement based on the sample weight against known certified elemental standards. The $\delta^{13}\text{C}$ values were corrected to the primary reference scale of Vienna Pee Dee Belemnite. Every fifth sample was duplicated for precision quality control/quality assurance. Three of the duplicate samples (two *C. canadensis*, one *P. australis*) were outside of the calibration range and were removed from the dataset, leaving seven duplicates for precision analysis. Analytical precision was measured using relative percent difference between duplicates (EPA 2014), and the average precision was 0.002% ($\pm$ 0.113 st. error) for $\delta^{13}\text{C}$, 3.25% ($\pm$ 3.12 st. error) for %C, 4.89% ($\pm$ 3.83 st. error) for %N.

Soil samples collected for resource measurements were dried at 80°C, ground into a homogenous mixture, then analyzed for soil pH, phosphorus (mg/Kg), carbon (% dry weight), total nitrogen (% dry weight), calcium (mg/Kg), potassium (mg/Kg), magnesium (mg/Kg), sodium (mg/Kg), copper (mg/Kg), iron (mg/Kg), zinc (mg/Kg dry), manganese (mg/Kg), and sulfur ($\mu\text{g/g}$). Plant available phosphorus was measured using sodium bicarbonate-extractable phosphorus following Reid (1998). Total nitrogen (TN) and carbon were measured using thermal conductivity detection (Reid 1998). The K, Mg, Ca, and Na samples were extracted using 1.0 N Ammonium Acetate solution, following Simard (1993). Copper, iron, and zinc samples were extracted using a 0.005M DTPA solution and the filtrate was analyzed by ICP-OES following Liang and Karamanos (1993). Manganese was measured using 0.1 N phosphoric acid as the extracting solution, following Reid (1998). For sulfur, homogenized samples were closed-vessel microwave digested with nitric acid and hydrochloric acid, then the microwave digested sample was brought to volume with Nanopure water and quantification was performed using ICP-OES (AOAC 2011.14). Nitrogen and carbon analyses were done at the Biogeochemical Analytical Service Laboratory at the University of Alberta while the other nutrient analyses were conducted by the Agriculture and Food Laboratory at the University of Guelph.

Statistical Analyses

We determined that year did not influence plant biomass (general linear model $F_{1,164} = 2.40$, $p = 0.123$) or carbon assimilation rates at full sunlight ($1500 \mu\text{mol s}^{-1} \text{m}^{-2}$) (general linear model $F_{1,164} = 0.004$, $p = 0.948$), so we pooled the data from both years for these variables. We used two-way ANOVAs to compare carbon assimilation rates and water use efficiency at $1500 \mu\text{mol s}^{-1} \text{m}^{-2}$ among species and between the treatments. We ran four models in total with either carbon assimilation rate or water use efficiency as the response variable, with an interaction between phytometer species (for resident phytometers) or phytometer neighbours (for *P. australis* phytometers) and treatment (with or without competition). We used the same model design to assess differences in $\delta^{13}\text{C}$. Duplicates in the $\delta^{13}\text{C}$ data were averaged to one value for analyses. We used Type III sums of squares, unless an interaction was not significant, then we report Type II sums of squares. If a fixed factor was significant, without a significant interaction term, we used Tukey's HSD post-hoc test to assess differences among levels of the factor. Analyses were performed using the *car* package (Fox and Weisberg 2019) and *agricolae* (de Mendiburu 2020).

To evaluate the allocation of resources to above-ground biomass between treatments, we compared the yield of phytometers growing with competition to those growing without competition. Using the phytometers that were paired by height at the beginning of the experiment, we calculated differences in above-ground yield using the relative competition index (RCI) approach (Grace 1995; Goldberg et al. 1999; Vilà and Weiner 2004):

$$(Y_{\text{without competition}} - Y_{\text{with competition}}) / Y_{\text{without competition}}$$

Yield (Y) represents the above-ground biomass of each phytometer. As the weights are standardized, values greater than 0, with a maximum of 1, indicate that the above-ground biomass of the plant growing with competition was lower than its counterpart growing without competition. Values < 0 indicate the above-ground biomass of the plant growing with competition was higher than its counterpart growing without competition. This allows us to compare the differences in above-ground yield among the species while accounting for variation in size among species.

The soil data, except pH and light, collected from the unmanipulated sites were converted to ppm (i.e., mg/Kg) and log transformed to improve normality. To control for collinearity among environmental variables, we summarized the underlying correlation structure using principal components analysis (PCA). We created a matrix of soil nutrients, pH, soil moisture, and proportion of incident PAR reaching the ground and conducted the PCA, with a correlation matrix, using the *rda* function in *vegan* (Oksanen et al. 2020). The PCA scores were then multiplied by the proportion of variance explained by each axis, to give them appropriate weight, and were used as an indicator of ecological niche to quantify trophic niche region and overlap among the plant species using *nicheROVER* (Lysy et al. 2017). To estimate pairwise niche overlap, *nicheROVER* employs a Bayesian framework to calculate the probability that an individual from species A is found in the niche region (a 95% probability region in multivariate space) of species B (Swanson et al. 2015). All analyses were performed using R v. 4.0.3 (R Core Team 2020).

Results

Resident species carbon assimilation rates

Carbon assimilation rates in resident species showed a marked effect of competition (Fig. 1). From PAR levels $200 \mu\text{mol s}^{-1} \text{m}^{-2}$ to $1500 \mu\text{mol s}^{-1} \text{m}^{-2}$ carbon assimilation rates were higher in resident species growing without above-ground competition with *P. australis* compared to those growing with competition (Fig. 1A). While there was no interaction between species and treatment (two-way ANOVA $F_{2,91} = 0.759$, $p = 0.471$), all three resident species had higher carbon assimilation rates at $1500 \mu\text{mol s}^{-1} \text{m}^{-2}$ PAR when they were growing without competition (two-way ANOVA $F_{1,91} = 33.52$, $p < 0.001$; Table 1 & 2). There was also a significant difference in carbon assimilation rates among the resident species (two-way ANOVA $F_{2,91} = 38.720$, $p < 0.001$). *Typha* spp. had carbon assimilation rates that were significantly higher than either *C. canadensis* or *C. aquatilis* (Table 1). Photosynthetic water use efficiency followed the same pattern as carbon assimilation rates (Table 1 & 2). Water use efficiency was higher in the treatments without competition, while *Typha* spp. had significantly higher WUE than *C. canadensis*, and the WUE of *C. aquatilis* was intermediate (Appendix E).

Phragmites australis carbon assimilation and water use efficiency

There was no difference in carbon assimilation rates for *P. australis* growing with or without competition (Fig. 1B). There was no significant interaction between neighbouring species or treatment (two-way ANOVA $F_{2,63} = 0.615$, $p = 0.544$), and neither treatment (two-way ANOVA $F_{1,63} = 2.80$, $p = 0.099$) or neighbouring species (two-way ANOVA $F_{2,63} = 1.459$, $p = 0.240$; Table 2) were significant predictors of carbon assimilation rates in *P. australis*. The average carbon assimilation rate of *P. australis* at $1500 \mu\text{mol s}^{-1} \text{m}^{-2}$ was similar to *Typha* spp., and considerably higher than *C. aquatilis* or *C. canadensis* (Table 1). Water use efficiency was significantly higher in the 'no competition' treatment (two-way ANOVA $F_{1,63} = 4.036$, $p = 0.0488$; Table 2) and, overall, was higher than the three resident species (Table 1 & Appendix E).

Above ground biomass & PAR

Unlike carbon assimilation, above-ground biomass did not exhibit a clear effect of competition. *Carex aquatilis* phytometers (average $0.156 (\pm 0.07 \text{ st. error})$) produced less above-ground biomass when growing with competition from *P. australis*. In contrast, *C. calamagrostis* (average $-0.651 (\pm 0.55 \text{ st. error})$) and *Typha* spp. (average $-0.002 (\pm 0.17 \text{ st. error})$) both produced more above-ground biomass when growing with competition from *P. australis*. All of the *P. australis* phytometers produced more above-ground biomass when growing with competition from *C. canadensis* (average RCI $-0.223 (\pm 0.22)$), *C. aquatilis* (average RCI $-0.329 (\pm 0.52)$) and *Typha* spp. (average RCI $-0.233 (\pm 0.16)$) (Appendix F).

The average amount of PAR reaching resident species and *P. australis* phytometers was higher when growing without competition (Table 1; Appendix G). Both *P. australis* (average height $156 \text{ cm} (\pm 2.99 \text{ st. error})$) and *Typha* spp. (average height $186 \text{ cm} (\pm 5.39 \text{ st. error})$) are larger species than resident meadow species *C. canadensis* (average height $93.1 \text{ cm} (\pm 1.68 \text{ st. error})$) and *C. aquatilis* (average height $98.9 \text{ cm} (\pm 1.59 \text{ st. error})$). As such, *P. australis* and *Typha* spp. generated more above-ground biomass (Table 1; Appendix G) and gained height more quickly over the field season than *C. canadensis* or *C. aquatilis*. On average, phytometers growing without competition were shorter than those growing with competition (Appendix H).

Resident species foliar nutrient content and isotopes

Overall, resident species in both treatments had lower nitrogen to carbon ratios than invasive *P. australis* phytometers growing without competition (Fig. 3A). Carbon content in the leaves of resident species did not have a significant interaction between species and treatment, nor was treatment significant (Table 2). However, there was a significant difference in carbon content among the species (two-way ANOVA $F_{2,23} = 27.31$, $p < 0.01$). The carbon content in *Typha* spp. was significantly higher than *C. aquatilis*, while *C. canadensis* was intermediate (Table 1). Nitrogen content in the leaves of resident species exhibited a significant interaction between species and treatment (two-way ANOVA $F_{2,23} = 3.770$, $p = 0.038$). Nitrogen content in *C. aquatilis* and *C. canadensis* increased when phytometers grew without competition, while *Typha* spp. nitrogen content decreased when growing without competition (Table 1).

There was no significant interaction between resident species and treatment for $\delta^{13}\text{C}$, but both species and treatment were significant predictors of $\delta^{13}\text{C}$ values (Table 2). The average $\delta^{13}\text{C}$ value in *Typha* spp. leaves was significantly lower than *C. aquatilis* and *C. canadensis* (Table 1). The average $\delta^{13}\text{C}$ value

for phytometers growing with competition was lower than those without competition.

Phragmites australis foliar nutrient content and isotopes

For *P. australis* phytometers, carbon content among neighbouring species did not differ between treatments, nor among neighbouring species ($F_{2,12} \leq 3.576$, $p \geq 0.083$; Fig. 2.3C, Table 2.2). The average carbon content in *P. australis* was lower than *Typha* spp., but similar to *C. aquatilis* (Table 1). The nitrogen content in *P. australis* phytometers differed significantly between treatments, but the interaction term and neighbours were not significant predictors (Table 2). The nitrogen content in phytometers growing without competition was significantly higher than those growing with competition (Table 1). The interaction term and fixed factors were not significant predictors of $\delta^{13}\text{C}$ values *P. australis* phytometers (Table 2).

Table 1. Averages and standard errors for response variables for each phytometer and treatment: percent of incident photosynthetically available radiation ($\mu\text{mol s}^{-1} \text{m}^{-2}$) (PAR) reaching each phytometer; the amount of above-ground biomass (g) generated by each phytometer; carbon assimilation rate ($\mu\text{mol CO}_2 \text{s}^{-1} \text{m}^{-2}$) (A) at 1500 $\mu\text{mol s}^{-1} \text{m}^{-2}$ PAR; water use efficiency ($\text{CO}_2 \text{mmol s}^{-1} \text{m}^{-2} \text{H}_2\text{O}$) (WUE) at 1500 $\mu\text{mol s}^{-1} \text{m}^{-2}$ PAR; foliar carbon (%C), foliar nitrogen (%N), and $\delta^{13}\text{C}$ values from leaves.

		<i>Calamagrostis canadensis</i>	<i>Carex aquatilis</i>	<i>Typha</i> spp.	<i>Phragmites australis</i> and <i>C. canadensis</i>	<i>Phragmites australis</i> and <i>C. aquatilis</i>	<i>Phragmites australis</i> and <i>Typha</i> spp.
PAR %	Without competition	67.0 ($\pm$ 6.51)	50.0 ($\pm$ 5.47)	90.0 ($\pm$ 2.14)	91.6 ($\pm$ 2.35)	90.6 ($\pm$ 2.00)	94.4 ($\pm$ 1.86)
	Competition	40.4 ($\pm$ 6.74)	41.4 ($\pm$ 6.78)	75.2 ($\pm$ 7.03)	77.3 ($\pm$ 8.37)	82.6 ($\pm$ 7.54)	93.7 ($\pm$ 1.63)
Biomass (g)	Without competition	2.24 ($\pm$ 0.541)	2.2 ($\pm$ 0.223)	38.8 ($\pm$ 2.38)	25.7 ($\pm$ 4.59)	16.7 ($\pm$ 2.19)	21.1 ($\pm$ 2.89)
	Competition	1.47 ($\pm$ 0.161)	2.0 ($\pm$ 0.305)	36.3 ($\pm$ 3.60)	27.8 ($\pm$ 4.96)	15.2 ($\pm$ 3.19)	19.6 ($\pm$ 2.32)
	Without competition	13.2 ($\pm$ 0.69)	14.9 ($\pm$ 0.94)	20.7 ($\pm$ 1.65)	18.8 ($\pm$ 0.91)	21.4 ($\pm$ 1.16)	19.9 ($\pm$ 1.09)
	Competition	8.7 ($\pm$ 0.51)	9.2 ($\pm$ 1.14)	17.6 ($\pm$ 1.28)	18.3 ($\pm$ 1.06)	18.3 ($\pm$ 1.03)	21.3 ($\pm$ 2.05)
WUE	Without competition	2.2 ($\pm$ 0.09)	2.44 ($\pm$ 0.09)	2.42 ($\pm$ 0.20)	3.11 ($\pm$ 0.16)	3.02 ($\pm$ 0.10)	3.32 ($\pm$ 0.14)
	Competition	1.9 ($\pm$ 0.09)	1.85 ($\pm$ 0.19)	2.35 ($\pm$ 0.12)	2.94 ($\pm$ 0.12)	2.82 ($\pm$ 0.08)	3.05 ($\pm$ 0.15)
C	Without competition	47.3 (0.82)	46.0 (0.16)	48.9 (0.55)	46.8 ($\pm$ 0.23)	46.1 ($\pm$ 0.62)	46.7 ($\pm$ 0.83)
	Competition	47.7 (0.70)	46.1 (0.56)	47.9 (0.61)	47.0 ($\pm$ 0.49)	47.4 ($\pm$ 0.47)	47.7 ($\pm$ 0.41)
N	Without competition	1.1 (0.10)	0.8 (0.10)	2.0 (0.24)	2.4 ($\pm$ 0.19)	2.6 ($\pm$ 0.13)	2.5 ($\pm$ 0.34)
	Competition	1.8 (0.09)	1.1 (0.16)	1.7 (0.28)	1.7 ($\pm$ 0.14)	1.8 ($\pm$ 0.06)	1.8 ($\pm$ 0.28)
$\delta^{13}\text{C}$	Without competition	-27.9 (0.51)	-28.8 (0.38)	-30.0 (0.36)	-26.5 ($\pm$ 0.66)	-26.4 ($\pm$ 0.60)	-26.1 ($\pm$ 0.44)
	Competition	-27.0 (0.39)	-27.8 (0.22)	-29.2 (0.28)	-27.0 ($\pm$ 0.50)	-27.0 ($\pm$ 0.16)	-26.4 ($\pm$ 0.40)

Table 2. ANOVA results for carbon assimilation ($\mu\text{mol CO}_2 \text{s}^{-1} \text{m}^{-2}$) (A) and water use efficiency ($\text{CO}_2 \text{mmol s}^{-1} \text{m}^{-2} \text{H}_2\text{O}$) (WUE) at 1500 $\mu\text{mol s}^{-1} \text{m}^{-2}$ PAR, percent carbon (%C), nitrogen (%N), and $\delta^{13}\text{C}$ values from phytometer leaves. Resident species phytometers (*C. aquatilis*, *C. canadensis*, *Typha* spp.) or *P. australis* phytometer neighbours (*C. aquatilis*, *C. canadensis*, *Typha* spp.) and treatment (with competition or without competition) as fixed factors.

Resident species phytometers										<i>Phragmites australis</i> phytometers										
Species			Treatment			Spp x Treatment			Residual	Neighbours			Treatment			Neighbour x Treatment			Residual	
df	F	p	df	F	p	df	F	p		df	F	p	df	F	p	df	F	p		
A	2	38.72	<0.001	1	33.52	<0.001	2	0.76	0.471	91	2	1.45	0.240	1	2.80	0.099	2	0.62	0.544	63
WUE	2	3.15	0.048	1	9.22	0.003	2	1.74	0.182	91	2	2.03	0.140	1	4.04	0.048	2	0.06	0.938	63
%C	2	8.23	0.002	1	0.138	0.714	2	0.730	0.493	23	2	0.32	0.730	1	3.58	0.083	2	0.57	0.581	12
%N	2	11.54	<0.001	1	6.32	0.019	2	3.77	0.038	23	2	0.46	0.641	1	18.78	<0.001	2	0.01	0.991	12
δ ¹³ C	2	17.92	<0.001	1	10.34	0.004	2	0.05	0.956	23	2	0.56	0.584	1	1.39	0.262	2	0.04	0.963	12

Niche space and niche overlap

The first two axes of the PCA accounted for 73.6% of the variance in the data (Axis 1: 0.648, Axis 2: 0.086 (Appendix I)), and were selected based on a scree plot assessing inertia (Appendix J). PCA axis 1 illustrates a clear gradient among the three resident species, reflecting the partitioning of their associated “remnant” vegetation communities along the water depth gradient (Fig. 3). *Calamagrostis canadensis* is on one end with the lowest average soil moisture (73.6 % (±1.53 st. error, coefficient of variation 8.1%)), while *C. aquatilis* (79.2% (± 0.93 st. error, coefficient of variation 4.5%)) and *Typha* spp. (82.0% (± 1.29 st. error, coefficient of variation 6.1%)) were typically inundated. *Phragmites australis* sites had greater variation in soil moisture, with an average of 78.2% but ± 3.84 st. error, coefficient of variation 19.0%. Soils where *Typha* spp. dominated also had the highest concentrations of phosphorus (35.6 mg/kg (± 5.23 st. error)), potassium (128.6 mg/kg (± 0.11 st. error)), and nitrogen (11,066.7 mg/kg (± 1277.26 st. error)), while soils where *C. canadensis* dominated had the lowest concentration of these three nutrients (P: 9.2 mg/Kg (± 0.75 st. error), K: 34.15 mg/kg (± 0.305 st. error), N: 1780 mg/kg (± 154.06 st. error)). PCA axis 2 seems to illustrate a gradient between incident light reaching the ground. The average incident PAR reaching the ground was 16.07% (± 5.81 st. error) in stands of *C. aquatilis*, 8.09% (± 2.09 st. error) in stands of *C. canadensis*, 6.21% (± 1.55 st. error) in stands of *Typha* spp., and 2.76% (± 0.83 st. error) in stands of *P. australis*.

Phragmites australis had the largest niche region of the four species, followed by *Typha* spp., *C. aquatilis*, then *C. canadensis* (Table 3). The probability of *P. australis* overlapping with the niche space of *C. aquatilis* and *Typha* spp. was higher than the probability of overlap with *C. canadensis*. However, the probability of overlap of the three resident species onto the niche of *P. australis* was considerably higher (Table 3, Appendix K).

Table 3. Estimated niche region size, with standard error, and median overlap of 95% niche region with 95% credible intervals for invasive *P. australis* and resident *C. canadensis*, *C. aquatilis*, and *Typha* spp. based on PCA scores. Values indicate the overlap probability of species A onto the niche of species B.

Species A	95% Niche Region	Species B	Median & 95% CI
<i>Calamagrostis canadensis</i>	0.077 (± 0.021)	<i>Carex aquatilis</i>	20.2 (0 – 83)
		<i>Typha</i> spp.	0.0 (0 – 34)
		<i>Phragmites australis</i>	83.6 (25 – 100)
<i>Carex aquatilis</i>	0.186 (± 0.048)	<i>Calamagrostis canadensis</i>	4.7 (0 – 18)
		<i>Typha</i> spp.	31.9 (0 – 34)
		<i>Phragmites australis</i>	94.9 (73 – 100)
<i>Typha</i> spp.	0.304 (± 0.083)	<i>Calamagrostis canadensis</i>	0.1 (0 – 2)
		<i>Carex aquatilis</i>	16.5 (3 – 51)
		<i>Phragmites australis</i>	53.4 (30 – 93)
<i>Phragmites australis</i>	0.360 (± 0.098)	<i>Calamagrostis canadensis</i>	8.3 (2 – 22)
		<i>Carex aquatilis</i>	64.3 (42 – 87)
		<i>Typha</i> spp.	53.5 (22 – 84)

Discussion

Detrimental invasive species should exhibit high niche overlap and large fitness differences with resident species (MacDougall et al. 2009). We quantified differences in photosynthetic performance, competition for photosynthetically active radiation, and niche overlap between a globally successful, model invasive species, *P. australis*, and resident wetland species. Our results confirm that *P. australis* has high niche overlap with resident plant species, is not negatively affected by competition for above-ground resources with resident species and utilizes available resources more effectively than resident species. Direct competition with *P. australis* significantly reduced the photosynthetic performance of resident species, while competition with resident species did not negatively impact *P. australis*. *Phragmites australis* also has the largest niche region and was most likely to overlap onto the niche of *C. aquatilis* and *Typha*. Resident species had a higher probability of overlapping onto the niche space of *P. australis*, particularly the meadow marsh species *C. canadensis* and *C. aquatilis*. This finding agrees with historical records of the region that identified meadow marsh and grass/sedge hummock were frequently displaced by *P.*

australis invasion (Wilcox et al. 2003). These results suggest *C. canadensis* and *C. aquatilis* could persist in areas currently dominated by *P. australis* if it were removed, and their absence is due to exclusion by this invasive plant. This study represents an advancement in testing the effects of fitness and niche differences in the success of a perennial, rhizomatous invasive plant.

The carbon assimilation rate and water use efficiency of all three resident species were lower than *P. australis* and showed a decrease when growing with above-ground competition. Meadow marsh species *C. canadensis* and *C. aquatilis* assimilated considerably less carbon and were less efficient at generating biomass per unit water transpired (Farquhar et al. 1989) than *P. australis*, and competition decreased carbon assimilation and water use efficiency further. Over the growing season *C. canadensis* and *C. aquatilis* produced less above-ground biomass and did not grow as tall or as fast as *P. australis*, a commonality among many species in *P. australis* invaded wetlands. In both freshwater and brackish marshes in North America, *P. australis* consistently produces more above-ground biomass than other wetland plants in the same system (Meyerson et al. 2000). *Typha*, however, also grows quickly, produces extensive above-ground biomass (Bansal et al. 2019), and has carbon assimilation rates similar to *P. australis*. However, *Typha* exhibited a decrease in carbon assimilation due to above-ground competition with *P. australis*, while *P. australis* competing with *Typha* did not. Our measurement of percent incident light in abundant stands of each species demonstrated that *P. australis* intercepts more photosynthetically active radiation than any of the resident species, including *Typha*. Similar work in freshwater marshes found the same pattern in monocultures and mixed stands of *Typha* and *P. australis* – approximately 30% of full sunlight reached the litter layer in *Typha* stands compared to 10% in *P. australis* stands – which the authors attribute to the horizontal orientation of *P. australis* leaves (Hirtreiter and Potts 2012). While these values are higher than what we measured, they also observed the pattern of *P. australis* intercepting more sunlight than *Typha*.

While *P. australis* produces dense stands that reduce light availability for other species, it is also subject to self-shading. Once stands have reached sufficient density, smaller and thinner shoots die prematurely from within-stand competition for light (van Der Toorn and Mook 1982; Hara et al. 1993). Our experimental design did not assess intraspecific competition for PAR, but we can assess each species' photosynthetic activity and whole plant function over the field season using $\delta^{13}\text{C}$ values (Dawson et al. 2002). *Phragmites australis* had the highest (least negative) $\delta^{13}\text{C}$ values ($-26.58\text{‰} \pm 0.18$ st. error), indicating enrichment with the heavier carbon atoms and more efficient photosynthesis over the growing season (Farquhar et al. 1989). Resident species had lower $\delta^{13}\text{C}$ values, and competition with *P. australis* resulted in lower average $\delta^{13}\text{C}$ values for all resident species, coinciding with their lower photosynthetic water use efficiency (Fry 1992). While water availability is not a limiting factor for wetland plants, balancing the trade-off between carbon gain and water loss to transpiration is under the biological control of plants via stomatal conductance. When growing with competition, resident plants were less efficient at generating biomass per unit water transpired (Farquhar et al. 1989). This reduced efficiency may further negatively affect plants growing in competition as they allocate more resources to above-ground growth.

Many of the resident species growing with competition produced more above-ground biomass or were taller than their counterparts growing without competition. Measuring above-ground biomass has been used to assess effects of competition in the field (e.g., Güsewell and Edwards 1999), however this approach appears to account for flexibility in resource allocation and plant plasticity. Plants can respond to low light availability by allocating more resources to above-ground tissue, such as height and leaf area (Weiner 2004; Craine and Dybzinski 2013) but this trade-off has consequences. Allocating more resources to above-ground tissue can result in reduced net carbon gain per individual, as observed in our measurements of carbon assimilation, and it can impede the acquisition of water and soil nutrients, resulting in a diminished overall competitive ability (Aschehoug et al. 2016). The low nitrogen content in the leaves of *C. canadensis* and *C. aquatilis* growing with competition appear to support this relationship between competition, re-allocation of resources, and nutrient uptake. Uddin and William (2018) found that *P. australis*-invaded sites had higher concentrations of available soil nutrients, including nitrogen and phosphorus, but *P. australis* produced extensive belowground biomass and usurped nutrients from neighbouring species. This competition for soil resources, coupled with the need to grow taller, results in particularly challenging conditions for meadow marsh species. In species-rich fens in Switzerland, shading from *P. australis* did not appear to affect the performance of native species (Güsewell and Edwards 1999). However, plant performance was evaluated by clipping above-ground biomass (Güsewell and Edwards 1999) and based on our results this work may have missed that plants were compensating for reduced carbon assimilation when growing with *P. australis* by allocating more resources to aboveground tissue production. Working in the field, we did not have the same level of environmental control and homogeneity in conditions that can be achieved in the greenhouse, but the patterns we observed in carbon assimilation and compensatory aboveground tissue production indicate that collecting above-ground biomass in the field does not tell the full story of plant interactions, especially for rhizomatous plants.

In addition to more efficient photosynthesis, *P. australis* had a higher nitrogen to carbon ratio when growing without competition than the other resident species. Nitrogen is used in the creation of chloroplasts (Evans 1989) and plants can maximize photosynthetic efficiency by allocating more nitrogen to sunny leaves high in the canopy (Hirose and Werger 1987). High foliar nitrogen is commonly noted in *P. australis* studies (e.g., Yuckin and Rooney 2019), suggesting *P. australis* is more efficient at nitrogen uptake than other wetland species (Farnsworth and Meyerson 2003). When growing with competition, *P. australis*, *C. aquatilis*, and *C. canadensis* had lower amounts of foliar nitrogen while *Typha* exhibited an increase in foliar nitrogen content when growing with competition. There are multiple reasons this seemingly anomalous pattern could occur. One hypothesis is that *C. canadensis* and *C. aquatilis* were N limited when growing in competition with *P. australis*, due either to its usurpation of available N or to dilution, as they increased aboveground tissue production to compensate for PAR interception by *P. australis*. In contrast, *Typha* may be compensating for reduced PAR by increasing chloroplast production. The strategic allocation by *Typha* of nitrogen only to leaves in full sunlight has been documented in the field, while *P. australis* allocated similar amounts of nitrogen to leaves down the entire canopy, resulting in low N use efficiency (Hirtreiter and Potts, 2012). We suggest that future work strategically assesses the distribution of foliar nitrogen throughout the canopy of these species when growing with or without competition, to further refine this mechanistic understanding.

Competition with *P. australis* has a detrimental effect on resident plants, and the niches of resident species are very likely to overlap with the niche of *P. australis*. Resident species' niches were aligned along a gradient of standing water, with *C. canadensis* in areas with the lowest soil moisture and low nutrient concentrations and *Typha* in areas of high soil moisture, deep standing water, and high nutrient concentrations. This is typical of wetland vegetation communities, which align themselves along a topographical or moisture gradient from inundated flooded areas to shallow standing water (Keddy 2010). Of

the three resident species, *Typha* had the largest niche region. *Typha x glauca* and *Typha angustifolia*, a parent species of *Typha x glauca*, both have a wide global range, proliferate in high nutrient environments, and generate monocultures that alter wetland communities (Bansal et al. 2019). The large niche region of *Typha* in our study agrees with the well-documented niche breadth of this species. *Typha x glauca* and *Typha angustifolia* are also obligate wetland plants that are well adapted to deeper water and require a degree of consistent flooding (Bansal et al. 2019). This explains the low probability of niche overlap between *Typha* and meadow species *C. aquatilis* and *C. canadensis*, which preferentially establish in areas with shallower seasonal inundation (Darris 2006; Tilley et al. 2011). The median probability of niche overlap between *Typha* and *P. australis* were nearly identical for each species. When monospecific stands of *Typha* and *P. australis* grow together, *P. australis* usually displaces *Typha* (Paradis et al. 2014). A component of this successful displacement is likely the negative effect that competition with *P. australis* has on *Typha* carbon assimilation. While *P. australis* and *Typha* have many similarities and are both considered invasive in North American wetlands (Galatowitsch et al. 1999), their interactions are likely mediated by environmental conditions. *Typha* spp. prefer a consistent level of inundation and do not thrive with variability (e.g., (Boers and Zedler 2008; Wilcox and Nichols 2008), while *P. australis* populations increase with variable water depths (e.g., Wilcox et al. 2003).

Understanding the specific outcomes of plant interactions can inform the patterns we observe in the field. However, the results of species interactions are often attributed to competition despite numerous other mechanisms that can confer an advantage to an introduced species (e.g., Richardson and Pyšek 2006). While these were outside the scope of our study, our work adds to the growing body of literature about *P. australis* (Meyerson et al. 2016) that can assist us in better understanding how resident communities resist invasion and how invasive species maintain their prominence once they become established. In particular, functional traits (i.e., annual plants) and the diversity of resident plant communities can result in niche pre-emption and niche partitioning that confers biological resistance to communities that would otherwise be invaded by *P. australis* at the seedling stage (Byun et al. 2013). We recommend future experiments test the role of functional traits (e.g., annual plants, perennial rhizomatous plants, high growth rate or biomass production, high carbon assimilation, leaf nitrogen content) on coexistence using *P. australis* stands to better replicate how *P. australis* expands clonally once established via seeds (e.g., Kettenring et al. 2016). The methods employed in Paradis et al. (2014) present a mesocosm approach that could be adapted for this purpose. Future work should also build on the study presented here by integrating population level changes over a longer time period and explicitly measuring the differences between interspecific competition and intraspecific competition (e.g., Chesson 2000). This will produce a more robust understanding of the processes that allow *P. australis* to remain abundant in an invaded marsh and give additional insight into which native North American species, if any, can stably coexist with *P. australis*.

We expect that throughout its range *P. australis* has high niche overlap with resident species, and likely has additional fitness advantages (e.g., faster nutrient uptake, reduced predation relative to native species) over the species that it is replacing in wetlands. For ecologists and wetland managers who may be interested in creating native plant communities that are resistant to *P. australis* invasion, the ability of *P. australis* to usurp nitrogen, intercept light, and assimilate carbon more efficiently than many native species and its high niche overlap should be considered. Selecting native species with traits such as fast growth early in the season and the ability to rapidly capture carbon and nitrogen may allow resident species to better persist alongside *P. australis*. Based on our results, preventing *P. australis* from invading freshwater wetland communities such as sedge meadow and meadow marsh is imperative, as the shorter vegetation and high niche overlap with *P. australis* makes them especially vulnerable to displacement.

Declarations

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Availability of data and material:

1. Robichaud, Courtney; Rooney, Rebecca (2021): Leaf nutrient and isotope data. figshare. Dataset. <https://doi.org/10.6084/m9.figshare.14737869.v2>
2. Robichaud, Courtney; Rooney, Rebecca (2021): Phytometer biomass. figshare. Dataset. <https://doi.org/10.6084/m9.figshare.14737878.v1>
3. Robichaud, Courtney; Rooney, Rebecca (2021): Niche resource measurements. figshare. Dataset. <https://doi.org/10.6084/m9.figshare.14737866.v1>
4. Robichaud, Courtney; Rooney, Rebecca (2021): Carbon assimilation and WUE. figshare. Dataset. <https://doi.org/10.6084/m9.figshare.14737857.v1>

Code availability: Not applicable

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Figures

Figure 1

The carbon assimilation rates ($\mu\text{mol CO}_2\text{ s}^{-1}\text{ m}^{-2}$) at varying levels of photosynthetically active radiation ($\mu\text{mol s}^{-1}\text{ m}^{-2}$) for resident plant species (A) and *P. australis* (B) with or without above-ground competition. Error bars represent standard error.

Figure 2

$\delta^{13}\text{C}$ values for each phytometer (A) and a scatter plot illustrating the carbon (%) and nitrogen (%) content in phytometer leaves (B). Large points with error bars represent the mean and standard error for each phytometer by treatment.

Figure 3

PCA using soil nutrients and percent incident light from marsh vegetation communities dominated by the target species: invasive *P. australis*, *C. canadensis* and *C. aquatilis* which represent remnant meadow marsh, and *Typha* spp. which represents remnant emergent marsh. The first two axes explain 75% of the variance in the data and were used to assess niche overlap among species. Ellipses are 90% confidence intervals for each group, and vectors represent all variables included in the PCA (Appendix I).

Supplementary Files

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