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. We measured differences in photosynthetic performance (carbon assimilation rate, $\delta^{13}C$, photosynthetic water use efficiency, biomass, light compensation point, light saturation point), canopy height and interception of 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 aboveground interspecific competition. Invasive *P. australis* intercepted more photosynthetically active radiation, had higher photosynthetic water use efficiency, a higher average light saturation point, 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.

Keywords  Interspecific competition · North America · Photosynthesis · Interactions · Wetland

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 favor the coexistence of seemingly similar species. The complexities of biological communities can make it difficult to predict the effects of invasive species.

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 (Minchin and Bertness 2003) and generates more biomass when grown in elevated CO\(_2\) 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 × glauca (Gogr. (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 × 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 × 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 and C”.

Once phytometers had matured (in July, but dates varied between years with interannual differences in weather), we measured the carbon assimilation rate (µmol CO₂ s⁻¹ m⁻²) (A) and photosynthetic water use efficiency (CO₂ mmol s⁻¹ m⁻² H₂O) (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 µmol s⁻¹ 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 µmol s⁻¹ 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 calculated the light compensation point (LCPT) and light saturation point (LSP) using a non-linear least squares regression of a non-rectangular hyperbola following Heberling et al. (2017). The LCPT is calculated as the x-intercept of the light response curve, while the LSP is the PAR level when 90% of the model asymptote (maximum carbon assimilation) is achieved (Heberling et al. 2017). Finally, we 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 near peak aboveground biomass in early August of 2016 and mid-July of 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 m 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, soil moisture using a WET sensor kit and HH2 moisture meter (Delta-T Devices, Burlington, ON) and 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 h 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 × 3 = 30 samples), and six P. australis phytometers (3 ‘with competition,’ 3 ‘without competition’) for each of the neighbouring species (6 × 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 δ13C isotopic composition of each selected leaf. The plants in our study are all C3 photosynthesizers which have δ13C values that range between -20 to -37‰ (Kohn 2010). The C3 photosynthetic pathway discriminates against the heavier 13C 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) δ13C 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 δ13C 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 δ13C 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 (Environmental Protection Agency (EPA) 2014), and the average precision was 0.002% (± 0.113 st. error) for δ13C, 3.25% (± 3.12 st. error) for %C, 4.89% (± 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 (mg/kg). 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 0.005 M 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 μmol s$^{-1}$ 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 μmol s$^{-1}$ m$^{-2}$ among species and between the competition treatments, including their interaction. We ran four models with carbon assimilation rate or water use efficiency at 1500 μmol s$^{-1}$ m$^{-2}$ as the response variables, with an
interaction between phytometer species (for resident phytometers) or phytometer neighbours (for \textit{P. australis} phytometers) and treatment (with or without competition). We used the same model design to assess differences in LCPT, LSP, and $\delta^{13}$C. Duplicates in the $\delta^{13}$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 \textit{car} package (Fox and Weisberg 2019) and \textit{agricolae} (de Mendiburu 2020).

We hypothesized that \textit{P. australis} might prove a superior competitor by having either a lower LCPT or a higher LSP than resident species growing in under the same edaphic and hydrologic conditions. We thus tested for differences in LCPT and LSP between resident species (combining phytometers with and without aboveground competition from \textit{P. australis}) and \textit{P. australis} growing in the same area (combining phytometers with and without aboveground competition from the equivalent resident species), using t-tests.

To evaluate the allocation of resources to aboveground 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 aboveground yield using the relative competition index (RCI) approach (Grace 1995; Goldberg et al. 1999; Vilà and Weiner 2004):

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

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. We carried out similar calculations to compare phytometer carbon assimilation at maximum irradiance and photosynthetic WUE with and without competition.

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 \textit{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 \textit{nicheROVER} (Lysy et al. 2017). To estimate pairwise niche overlap, \textit{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).

\section*{Results}

Resident species photosynthetic parameters

Photosynthetic parameters evaluated included photosynthetic WUE, carbon assimilation at 1500 $\mu$mol PAR s$^{-1}$ m$^{-2}$, light compensation points (LCPT) and light saturation points (LSP). Comparisons of carbon assimilation rates at 1500 $\mu$mol PAR s$^{-1}$ m$^{-2}$ demonstrated a stronger effect of interspecific competition on resident species than on \textit{P. australis}, evidenced by positive RCI-type values (Table 1). Interspecific competition with \textit{P. australis} reduced carbon assimilation rates at 1500 $\mu$mol PAR s$^{-1}$ m$^{-2}$ and greater (Fig. 1). At the maximum irradiance value of 1500 $\mu$mol PAR s$^{-1}$ m$^{-2}$, both carbon assimilation and photosynthetic WUE were lower in resident species in competition with \textit{P. australis} (Table 2), though for \textit{Typha} spp., the effect of interspecific competition with \textit{P. australis} on WUE was negligible (Table 1; “Appendix E”). Table 3 confirms that interspecific competition with \textit{P.}
australis significantly reduced carbon assimilation (p < 0.001) and WUE (p = 0.003) rates at 1500 μmol PAR s\(^{-1}\) m\(^{-2}\). These photosynthetic parameters also differed significantly among resident species (Table 3),
through the values of resident species were lower than the carbon assimilation and WUE by *P. australis* (Table 2, Fig. 1, “Appendix E”).

In contrast, LCPTs and LSPs did not differ significantly between phytometers growing with or without competition (“Appendix F”, G, H; p > 0.800) or among resident species (p > 0.330). However, resident species tended to have lower LSPs than *P. australis* phytometers growing nearby (“Appendix I”), specifically *C. aquatilis* (p < 0.001) and *Typha* spp. (p = 0.044).

### Phragmites australis photosynthetic parameters

The effect of competition with resident species on *P. australis* carbon assimilation and photosynthetic WUE at 1500 µmol PAR s⁻¹ m⁻² was relatively minor compared to the effects of interspecific competition with *P. australis* on resident species (Table 1). Indeed, although the values of carbon assimilation tended to be lower in *P. australis* growing in competition with resident species (Table 2), the differences were not statistically significant (Table 3). The effect of interspecific competition did have a significant (p = 0.048) effect on *P. australis* WUE,

|                            | Calamagrostis canadensis | Carex aquatilis | Typha spp. | Phragmites australis with *C. canadensis* | Phragmites australis with *C. aquatilis* | Phragmites australis with *Typha* spp. |
|-----------------------------|--------------------------|----------------|------------|-------------------------------------------|------------------------------------------|----------------------------------------|
| PAR %                       |                          |                |            |                                           |                                          |                                        |
| Without competition         | 67.0 (± 6.51)            | 50.0 (± 5.47)  | 90.0 (± 2.14) | 91.6 (± 2.35)                             | 90.6 (± 2.00)                           | 94.4 (± 1.86)                          |
| Competition                 | 40.4 (± 6.74)            | 41.4 (± 6.78)  | 75.2 (± 7.03) | 77.3 (± 8.37)                             | 82.6 (± 7.54)                           | 93.7 (± 1.63)                          |
| Biomass (g)                 | 2.24 (± 0.541)           | 2.2 (± 0.223)  | 38.8 (± 2.38) | 25.7 (± 4.59)                             | 16.7 (± 2.19)                           | 21.1 (± 2.89)                          |
| Without competition         | 2.0 (± 0.305)            | 36.3 (± 3.60)  | 27.8 (± 4.96) | 15.2 (± 3.19)                             | 19.6 (± 2.32)                           |                                        |
| Competition                 | 1.47 (± 0.161)           | 1.8 (± 2.5)    | 8.7 (± 1.65)  | 18.3 (± 1.06)                             | 18.3 (± 1.03)                           | 21.3 (± 2.05)                          |
| A                           | 13.2 (± 0.69)            | 14.9 (± 0.94)  | 20.7 (± 1.65) | 18.8 (± 0.91)                             | 21.4 (± 1.16)                           | 19.9 (± 1.09)                          |
| Without competition         | 9.2 (± 1.14)             | 17.6 (± 1.28)  | 18.3 (± 1.06) | 18.3 (± 1.03)                             | 21.3 (± 2.05)                           |                                        |
| Competition                 | 2.2 (± 0.09)             | 2.44 (± 0.09)  | 2.82 (± 0.08) | 3.02 (± 0.10)                             | 3.32 (± 0.14)                           |                                        |
| WUE                         |                          |                |            |                                           |                                          |                                        |
| Without competition         | 1.9 (± 0.09)             | 1.85 (± 0.19)  | 2.94 (± 0.12) | 2.82 (± 0.08)                             | 3.05 (± 0.15)                           |                                        |
| Competition                 | 47.3 (0.82)              | 46.0 (0.16)    | 46.8 (0.23)  | 46.1 (0.62)                               | 46.7 (0.83)                             |                                        |
| %C                          |                          |                |            |                                           |                                          |                                        |
| Without competition         | 47.7 (0.70)              | 46.1 (0.56)    | 47.0 (0.49)  | 47.4 (0.47)                               | 47.7 (0.41)                             |                                        |
| Competition                 | 1.1 (0.10)               | 0.8 (0.10)     | 2.0 (0.24)  | 2.4 (± 0.19)                             | 2.6 (± 0.13)                           | 2.5 (± 0.34)                          |
| %N                          |                          |                |            |                                           |                                          |                                        |
| Without competition         | 1.8 (0.09)               | 1.1 (0.16)     | 1.7 (± 0.28) | 1.7 (± 0.14)                             | 1.8 (± 0.06)                           | 1.8 (± 0.28)                          |
| Competition                 | - 27.9 (0.51)            | - 28.6 (0.38)  | - 30.0 (0.36) | - 26.5 (± 0.66)                           | - 26.4 (± 0.60)                        | - 26.1 (± 0.44)                        |
| δ¹³C                        |                          |                |            |                                           |                                          |                                        |
| Without competition         | - 27.0 (0.39)            | - 27.8 (0.22)  | - 29.2 (0.28) | - 27.0 (± 0.50)                           | - 27.0 (± 0.16)                        | - 26.4 (± 0.40)                        |
| Competition                 |                            |                |            |                                           |                                          |                                        |

*Phragmites australis* phytometers grew with each of the resident species as neighbours.
Table 3  ANOVA results for carbon assimilation (μmol CO₂ s⁻¹ m⁻²) (A) and photosynthetic water use efficiency (CO₂ mmol s⁻¹ m⁻² H₂O) (WUE) at 1500 μmol s⁻¹ m⁻² PAR, percent carbon (%C), nitrogen (%N), and δ¹³C values from phytometer leaves

|                | Resident species phytometers | Phragmites australis phytometers |
|----------------|-----------------------------|----------------------------------|
|                | Species | Competition | Spp. × Treatment | Residual | Neighbours | Competition | Neighbour × Treatment | Residual |
|                | 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      |
| δ¹³C           | 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      |

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.
particularly evident when it was competing with *Typha* spp. or *C. aquatilis*, which grow in deeper water (“Appendix E”).

The LSP of *P. australis* was significantly higher than that of resident *Typha* spp. (*p = 0.044*) and *C. aquatilis* (*p < 0.001*) growing nearby, though indistinguishable from that of *C. canadensis* (*p = 0.097*; “Appendix I”). Further, *P. australis* LSP was not predicted by treatment or neighbouring species (“Appendix G”; *p > 0.800*). LCPTs of *P. australis* phytometers did not differ between competition treatments (“Appendix G”; *p = 0.243*), but did differ depending on which resident species constituted the neighbor, with the LCPT for *P. australis* growing with *C. aquatilis* significantly higher than that of *P. australis* growing with *Typha* spp. (“Appendix G”; *p = 0.031*).

Above ground biomass, height and PAR

*Carex aquatilis* phytometers (average RCI: 0.156 (± 0.07 st. error)) produced less above-ground biomass when growing with competition from *P. australis*. In contrast, *C. calamagrostis* (average RCI: -0.651 (± 0.55 st. error)) and *Typha* spp. (average RCI: -0.002 (± 0.17 st. error)) both produced more above-ground biomass when growing with competition from *P. australis* (Table 1). All of the *P. australis* phytometers produced more above-ground biomass when growing with competition from *C. canadensis* (average RCI: 0.223 (± 0.22)), *C. aquatilis* (average RCI: -0.329 (± 0.52)) or *Typha* spp. (average RCI: -0.323 (± 0.16)) (Table 1).

Both *P. australis* (average height 156 cm (± 2.99 st. error)) and *Typha* spp. (average height 186 cm (± 5.39 st. error)) are taller species than resident meadow species *C. canadensis* (average height 93.1 cm (± 1.68 st. error)) and *C. aquatilis* (average height 98.9 cm (± 1.59 st. error)). As such, *P. australis* and *Typha* spp. generated more above-ground biomass (Table 1; “Appendix J”) and gained height more quickly over the field season than *C. canadensis* or *C. aquatilis* (“Appendix B, C, K”). On average, phytometers growing without competition reached lesser peak heights than those growing with competition (“Appendix K”).

The average percent of incident PAR reaching resident species and *P. australis* phytometers was higher when growing without competition (Table 2; “Appendix J”). However, the incertecption of PAR by neighbours was asymmetric, with *P. australis* neighbours shading resident species phytometers to a greater degree than the resident species neighbours shaded *P. australis* phytometers (Appendix J).

Resident species foliar nutrient content and isotopes

There was no significant interaction between resident species and competition treatment for δ13C, but both species and treatment were significant predictors of δ13C values separately (Table 3). The average δ13C value in *Typha* spp. leaves was the lowest, while average δ13C values were lower in phytometers growing with competition (Fig. 2A). Overall, resident species in both treatments had lower nitrogen to carbon ratios than invasive *P. australis* phytometers growing without competition. Carbon content in the leaves of resident species did not have a significant interaction between species and treatment, nor was the effect of competition significant (Table 3). However, there was a significant difference in carbon content among the species (two-way ANOVA F2,23 = 27.31, *p < 0.01*), with carbon content highest in *Typha* spp. (Table 2). Nitrogen content in the leaves of resident species exhibited a significant interaction between species and treatment (two-way ANOVA F2,23 = 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 2).

*Phragmites australis* foliar nutrient content and isotopes

The carbon content of *P. australis* did exhibit a significant interaction effect nor did it differ among neighbouring species (F2,12 ≤ 3.576, *p ≥ 0.083*; Fig. 2B, Table 3). However, the nitrogen content in *P. australis* phytometers differed significantly between treatments, and was significantly higher in phytometers growing without competition (Fig. 2C, Table 1). The interaction term and fixed factors were not significant predictors of δ13C values *P. australis* phytometers (Table 3).
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 L’’)], and were selected based on a scree plot assessing inertia (“Appendix M’’). 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,* and *C. canadensis*.

**Fig. 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).
then *C. canadensis* (Table 4). 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 N”).

**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 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* to the same degree. *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 from our study area 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 areas currently dominated by *P. australis* if it were removed and environmental conditions were otherwise favourable. 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*. 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*. The light saturation points (LSP) of resident *C. aquatilis* and *Typha* spp. phytometers were also significantly lower than those of nearby *P. australis*, substantiating the hypothesis that *P. australis* can outcompete resident species through superior growth but is not able to acclimate to shade (Jespersen et al. 2021). However, light compensation points (LCPT) did not differ between resident species and nearby *P. australis* phytometers, indicating *P. australis* does not benefit

### Table 4

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

Values indicate the overlap probability of species A onto the niche of species B.
from lower respiration rates or greater photosynthetic efficiency than resident species (Mathur et al. 2018). 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). This height advantages P. australis, especially as recent work in tidal marshes determined that P. australis has a low ability to acclimate to shade (Jespersen et al. 2021). 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 aboveground competition with P. australis, while P. australis competing with Typha did not. Indeed, phytometers of all three resident species exhibited relatively lower carbon assimilation rates and water use efficiencies when growing with aboveground competition from P. australis. 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.

Given that competition with P. australis led to greater shading of resident species phytometers, we anticipated that shade adaptation might be a suitable analogy for understanding the effects of interspecific competition with P. australis on resident species. For example, shade-adapted leaves typically have lower respiration rates leading to lower LCPT values and they maximize light capture at the risk of photoinhibition leading to lower LSP values (Mathur et al. 2018). However, our data did not support this, as we did not observe significant differences in LCPT or LSP between phytometers growing with and without competition.

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; Harada et al. 1993). Our experimental design did not assess intraspecific competition for PAR, though future experiments incorporating intraspecific competition would delineate the boundaries of potential coexistence of invasive P. australis and resident species. Despite this limitation, we can assess each species’ photosynthetic activity and whole plant function over the field season using δ13C values (Dawson et al. 2002). Phragmites australis had the highest (least negative) δ13C values (−26.58% ± 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 δ13C values, and competition with P. australis resulted in lower average δ15C 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 phytometers 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 × glauca* and *Typha angustifolia*, a parent species of *Typha × 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 × 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 Zeddler 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. To improve our mechanistic understanding of plant invasions, we suggest future research repeats our experiment across a larger geographic area to test how these interspecific interactions vary over the range of P. australis invasion in North America. 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.

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Availability of data and material Robichaud and Rooney (2021): Leaf nutrient and isotope data. figshare. Dataset. https://doi.org/10.6084/m9.figshare.14737869.v2. Robichaud and Rooney (2021): Phytometer biomass. figshare. Dataset. https://doi.org/10.6084/m9.figshare.14737878.v1. Robichaud and Rooney (2021): Niche resource measurements. figshare. Dataset. https://doi.org/10.6084/m9.figshare.14737866.v1. Robichaud and Rooney (2021): Carbon assimilation and WUE. figshare. Dataset. https://doi.org/10.6084/m9.figshare.14737857.v1.
Code availability  Code for light response curves available on GitHub (https://github.com/cdrobich/Robichaud_Rooney_BiolInv).

Declarations

Conflict of interest  The authors have no competing interests to declare.

Appendix A

Location of the 96 plots in Long Point, ON established in 2017 (A) and an illustration of what plots (B). Each plot consisted of one phytometer (one individual plant of each species) grown either with or without above-ground competition from *P. australis*, or one of the three resident species. The location of 2016 plots were nearly identical to the 2017 layout. Inset maps illustrate the location of the plots in Long Point, with a polygon indicating the area from which the environmental measures were taken from unmanipulated areas of each target species, and the location of the study in the Great Lakes region.
Appendix B

Phytometer height over the 2016 field season. Not collected (NC) indicates when a phytometer had died or was consumed. If above-ground tissue was still present, then it was measured and collected at the end of the growing season. Occasionally phytometers did not possess a whole, entire leaf for carbon assimilation measurements. See also Appendix K. We took the last height measures two weeks before we terminated the experiment and harvested phytometers for above-ground biomass in early August.

| ID    | Phytometer | Neighbours | Competition | 18-May-16 | 03-Jun-16 | 12-Jun-16 | 22-Jun-16 | 02-Jul-16 | 12-Jul-16 |
|-------|------------|------------|-------------|-----------|-----------|-----------|-----------|-----------|-----------|
| PCC1CU| Phragmites | Calamagrostis | No         | 63        | 160       | 183       | 216       | 230       | 248       |
| PCC2CU| Phragmites | Calamagrostis | No         | 41        | 98        | 110       | 126       | 129       | 145       |
| PCC1  | Phragmites | Calamagrostis | Yes        | 60        | 128       | 155       | 173       | 183       | 188       |
| PCC2  | Phragmites | Calamagrostis | Yes        | 42        | 100       | 124       | 141       | 149       | 160       |
| PCC3CU| Phragmites | Calamagrostis | No         | 52        | 127       | 145       | 166       | 180       | 194       |
| CAP1CU| Carex      | Phragmites  | No         | 61        | 92        | 91        | 100       | 101       | 98        |
| CAP1  | Carex      | Phragmites  | Yes        | 61        | 92        | 97        | 97        | 97        | 97        |
| CAP2CU| Carex      | Phragmites  | No         | 71        | 80        | 86        | 91        | 89        | 90        |
| CAP2  | Carex      | Phragmites  | Yes        | 70        | 91        | 93        | 95        | 93        | 93        |
| CAP3CU| Carex      | Phragmites  | No         | 70        | 106       | 107       | 103       | 112       | 110       |
| CAP3  | Carex      | Phragmites  | Yes        | 70        | 99        | 105       | 105       | 104       | 103       |
| CAP4CU| Carex      | Phragmites  | No         | 64        | 105       | 114       | 111       | 111       | NC        |
| CAP4  | Carex      | Phragmites  | Yes        | 61        | 105       | 112       | 113       | 113       | 114       |
| CAP5CU| Carex      | Phragmites  | No         | 83        | 90        | 94        | 94        | 95        | 90        |
| CAP5  | Carex      | Phragmites  | Yes        | 82        | 100       | 104       | 106       | 107       | 100       |
| PCC3  | Phragmites | Calamagrostis | Yes        | 52        | 138       | 153       | 167       | 174       | 192       |
| PCC4CU| Phragmites | Calamagrostis | No         | 75        | 190       | 222       | 243       | 261       | 279       |
| PCC4  | Phragmites | Calamagrostis | Yes        | 78        | 191       | 214       | 245       | 258       | 272       |
| PCC5CU| Phragmites | Calamagrostis | No         | 63        | 174       | 202       | 230       | 249       | 264       |
| PCC5  | Phragmites | Calamagrostis | Yes        | 64        | 160       | 185       | 212       | 231       | 243       |
| PCC6CU| Phragmites | Calamagrostis | No         | 69        | 122       | 132       | 146       | 156       | 166       |
| PCC6  | Phragmites | Calamagrostis | Yes        | 65        | 159       | 178       | 209       | 220       | 223       |
| CCP1CU| Calamagrostis | Phragmites  | No         | 66        | 106       | 114       | 120       | 123       | 124       |
| CCP1  | Calamagrostis | Phragmites  | Yes        | 67        | 93        | 98        | 109       | 114       | 114       |
| CCP2CU| Calamagrostis | Phragmites  | No         | 65        | 83        | 90        | NC        | NC        | NC        |
| CCP2  | Calamagrostis | Phragmites  | Yes        | 79        | 113       | 119       | 131       | 134       | 137       |
| CCP3CU| Calamagrostis | Phragmites  | No         | 67        | 108       | 129       | 139       | NC        | NC        |
| CCP3  | Calamagrostis | Phragmites  | Yes        | 61        | 89        | 97        | 101       | 101       | 103       |
| CCP4CU| Calamagrostis | Phragmites  | No         | 58        | 77        | 82        | 85        | 79        | NC        |
| CAP6CU| Carex      | Phragmites  | No         | 59        | 85        | 96        | 108       | 108       | 112       |
| CAP6  | Carex      | Phragmites  | Yes        | 63        | 105       | 100       | 100       | 101       | 100       |
| CAP7CU| Carex      | Phragmites  | No         | 62        | 78        | 102       | 111       | 106       | 109       |
| CAP7  | Carex      | Phragmites  | Yes        | 63        | 103       | 114       | 120       | 119       | 119       |
| CAP8CU| Carex      | Phragmites  | No         | 53        | 83        | 82        | 89        | 85        | 84        |
| CAP8  | Carex      | Phragmites  | Yes        | 51        | 81        | 86        | 86        | 86        | 86        |
| CAP9CU| Carex      | Phragmites  | No         | 71        | 96        | 98        | 99        | 100       | 102       |
| CAP9  | Carex      | Phragmites  | Yes        | 73        | 109       | 110       | 113       | 111       | 111       |
| ID    | Phytometer | Neighbours | Competition   | 18-May-16 | 03-Jun-16 | 12-Jun-16 | 22-Jun-16 | 02-Jul-16 | 12-Jul-16 |
|-------|------------|------------|---------------|-----------|-----------|-----------|-----------|-----------|-----------|
| CAP10CU | Carex     | Phragmites | No            | 80        | 88        | 100       | 104       | 100       | 105       |
| CAP10  | Carex     | Phragmites | Yes           | 79        | 93        | 99        | 99        | 100       | 100       |
| PCA1CU  | Phragmites | Carex     | No            | 86        | 149       | 171       | 194       | 208       | 223       |
| PCA1   | Phragmites | Carex     | Yes           | 85        | 116       | 130       | 142       | 154       | 164       |
| PCA2CU  | Phragmites | Carex     | No            | 80        | 122       | 131       | 148       | NC        | NC        |
| PCA2   | Phragmites | Carex     | Yes           | 80        | 169       | 197       | 227       | 246       | 255       |
| PCA3CU  | Phragmites | Carex     | No            | 69        | 140       | 155       | 175       | 194       | 215       |
| PCA3   | Phragmites | Carex     | Yes           | 68        | 109       | 123       | 137       | 145       | 160       |
| PCA4CU  | Phragmites | Carex     | No            | 83        | 130       | 141       | 154       | 176       | 191       |
| PCA4   | Phragmites | Carex     | Yes           | 85        | 133       | 148       | 164       | 175       | 182       |
| PCA5CU  | Phragmites | Carex     | No            | 83        | 108       | NC        | NC        | NC        | NC        |
| PCA5   | Phragmites | Carex     | Yes           | 84        | 150       | 163       | 179       | 188       | 201       |
| PCA6CU  | Phragmites | Carex     | No            | 81        | 120       | 133       | 143       | 148       | 161       |
| PCA6   | Phragmites | Carex     | Yes           | 83        | 146       | 159       | 175       | 189       | 197       |
| CAP11CU | Carex     | Phragmites | No            | 87        | 91        | 97        | 97        | 97        | 97        |
| CAP11  | Carex     | Phragmites | Yes           | 84        | 88        | 91        | 92        | 92        | 89        |
| CAP12CU | Carex     | Phragmites | No            | 88        | 88        | 98        | 98        | 103       | 103       |
| CAP12  | Carex     | Phragmites | Yes           | 89        | 103       | 108       | 97        | 95        | 108       |
| CCP4   | Calamagrostis | Phragmites | Yes         | 86        | 116       | 141       | 174       | 190       | 191       |
| CCP5CU | Calamagrostis | Phragmites | No          | 82        | 109       | 139       | 137       | NC        | NC        |
| CCP5   | Calamagrostis | Phragmites | Yes         | 83        | 121       | 133       | 161       | 169       | 171       |
| CCP6CU | Calamagrostis | Phragmites | No          | 55        | 78        | 88        | 94        | 100       | 101       |
| CCP6   | Calamagrostis | Phragmites | Yes         | 57        | 78        | 83        | 89        | 94        | 97        |
| CCP7CU | Calamagrostis | Phragmites | No          | 55        | 61        | 68        | 74        | 78        | 80        |
| CCP7   | Calamagrostis | Phragmites | Yes         | 56        | 79        | 78        | 80        | 82        | 83        |
| CCP8CU | Calamagrostis | Phragmites | No          | 45        | 75        | 79        | 83        | 85        | 85        |
| CCP8   | Calamagrostis | Phragmites | Yes         | 43        | 74        | 79        | 87        | 90        | 90        |
| CCP9CU | Calamagrostis | Phragmites | No          | 62        | 89        | 91        | 95        | 100       | 103       |
| CCP9   | Calamagrostis | Phragmites | Yes         | 63        | 78        | 81        | 89        | 94        | 98        |
| CCP10CU | Calamagrostis | Phragmites | No          | 57        | 92        | 87        | 110       | 110       | 121       |
| CCP10  | Calamagrostis | Phragmites | Yes         | 58        | 78        | 79        | 80        | 81        | 84        |
| CCP11CU | Calamagrostis | Phragmites | No          | 55        | 64        | 64        | 65        | 66        | 66        |
| CCP11  | Calamagrostis | Phragmites | Yes         | 53        | 54        | 74        | 57        | 59        | 63        |
| CCP12CU | Calamagrostis | Phragmites | No          | 68        | 94        | 101       | 109       | 110       | NC        |
| TYP1CU | Typha      | Phragmites | No           | 85        | 152       | 167       | 185       | 194       | 199       |
| TYP1   | Typha      | Phragmites | Yes          | 86        | 154       | 180       | 215       | 228       | 239       |
| TYP2CU | Typha      | Phragmites | No           | 78        | 140       | 174       | 200       | 213       | 217       |
| TYP2   | Typha      | Phragmites | Yes          | 82        | 168       | 193       | 229       | 232       | 245       |
| TYP3CU | Typha      | Phragmites | No           | 88        | 153       | 170       | 188       | 198       | 205       |
| TYP3   | Typha      | Phragmites | Yes          | 85        | 133       | 133       | 133       | 136       | 137       |
| TYP4CU | Typha      | Phragmites | No           | 92        | 170       | 187       | 227       | 227       | 248       |
| TYP4   | Typha      | Phragmites | Yes          | 94        | 176       | 200       | 221       | 237       | 259       |
| TYP5CU | Typha      | Phragmites | No           | 98        | 180       | 197       | 229       | 246       | 258       |
| TYP5   | Typha      | Phragmites | Yes          | 99        | 194       | 208       | 233       | 250       | 272       |
Phytometer height over the 2017 field season. Not collected (NC) indicates when a phytometer had died or was consumed. If above-ground tissue was still present, it was measured and collected at the end of the growing season. Occasionally phytometers did not possess a whole, entire leaf for carbon assimilation measurements. See also Appendix K. We took the last height measures two weeks before we terminated the experiment and harvested phytometers for above-ground biomass in mid-July.

### Appendix C

| ID     | Phytometer | Neighbours | Competition     | 18-May-16 | 03-Jun-16 | 12-Jun-16 | 22-Jun-16 | 02-Jul-16 | 12-Jul-16 |
|--------|------------|------------|----------------|-----------|-----------|-----------|-----------|-----------|-----------|
| TYP6CU | Typha      | Phragmites | No             | 98        | 185       | 200       | 211       | 242       | 256       |
| TYP6   | Typha      | Phragmites | Yes            | 97        | 172       | 194       | 200       | 235       | 270       |
| PTY1CU | Phragmites | Typha      | No             | 81        | 147       | 158       | 174       | 196       | 213       |
| PTY1   | Phragmites | Typha      | Yes            | 83        | 139       | 168       | 186       | 198       | 217       |
| PTY2CU | Phragmites | Typha      | No             | 93        | 147       | 155       | 169       | 193       | 203       |
| PTY2   | Phragmites | Typha      | Yes            | 92        | 170       | 180       | 211       | 221       | 238       |
| PTY3CU | Phragmites | Typha      | No             | 85        | 108       | 124       | 141       | 157       | NC        |
| PTY3   | Phragmites | Typha      | Yes            | 90        | 156       | 157       | 181       | 202       | 223       |
| PTY4CU | Phragmites | Typha      | No             | 98        | 181       | 198       | 212       | 231       | 249       |
| PTY4   | Phragmites | Typha      | Yes            | 95        | 165       | 180       | 196       | 218       | 234       |
| PTY5CU | Phragmites | Typha      | No             | 87        | 178       | 198       | 221       | 247       | 263       |
| PTY5   | Phragmites | Typha      | Yes            | 99        | 181       | 192       | 222       | 243       | 262       |
| PTY6CU | Phragmites | Typha      | No             | 112       | 174       | 192       | 213       | 228       | 242       |
| PTY6   | Phragmites | Typha      | Yes            | 117       | 209       | 228       | 259       | 278       | 298       |

| ID     | Phytometer | Neighbour | Competition    | 10-May-17 | 27-May-17 | 07-Jun-17 | 16-Jun-17 | 28-Jun-17 |
|--------|------------|-----------|----------------|-----------|-----------|-----------|-----------|-----------|
| CAP1   | Carex      | Phragmites| Yes            | 34        | 82        | 75        | 132       | 140       |
| CAP10  | Carex      | Phragmites| Yes            | 76        | 117       | 127       | 150       | 210       |
| CAP10CU| Carex      | Phragmites| No             | 77        | 108       | 104       | 142       | 150       |
| CAP11  | Carex      | Phragmites| Yes            | 79        | 98        | 120       | 141       | 160       |
| CAP11CU| Carex      | Phragmites| No             | 80        | 100       | 63        | 60        | 61        |
| CAP12  | Carex      | Phragmites| Yes            | 71        | 91        | 104       | 103       | 118       |
| CAP12CU| Carex      | Phragmites| No             | 66        | 82        | 91        | 95        | 120       |
| CAP1CU | Carex      | Phragmites| No             | 35        | 75        | 70        | 131       | 130       |
| CAP2   | Carex      | Phragmites| Yes            | 55        | 90        | 97        | 116       | 140       |
| CAP2CU | Carex      | Phragmites| No             | 57        | 91        | 96        | 127       | 127       |
| CAP3   | Carex      | Phragmites| Yes            | 63        | 105       | 86        | 123       | 125       |
| CAP3CU | Carex      | Phragmites| No             | 61        | 75        | 82        | 115       | 135       |
| CAP4   | Carex      | Phragmites| Yes            | 55        | 92        | 81        | 146       | 156       |
| CAP4CU | Carex      | Phragmites| No             | 52        | 70        | 80        | 141       | 143       |
| CAP5   | Carex      | Phragmites| Yes            | 72        | 118       | 89        | 144       | 153       |
| CAP5CU | Carex      | Phragmites| No             | 75        | 89        | 90        | 141       | 158       |
| CAP6   | Carex      | Phragmites| Yes            | 80        | 114       | 100       | 154       | 163       |
| CAP6CU | Carex      | Phragmites| No             | 81        | 95        | 103       | 142       | 145       |
| ID   | Phytometer | Neighbour | Competition | 10-May-17 | 27-May-17 | 07-Jun-17 | 16-Jun-17 | 28-Jun-17 |
|------|------------|-----------|-------------|-----------|-----------|-----------|-----------|-----------|
| CAP7 | Carex      | Phragmites| Yes         | 53        | 90        | 104       | 131       | 135       |
| CAP7CU| Carex       | Phragmites| No          | 51        | 71        | 95        | 155       | 140       |
| CAP8 | Carex      | Phragmites| Yes         | 66        | 96        | 93        | 134       | 138       |
| CAP8CU| Carex     | Phragmites| No          | 63        | 76        | 80        | 130       | 131       |
| CAP9 | Carex      | Phragmites| Yes         | 67        | 108       | 103       | 140       | 160       |
| CAP9CU| Carex      | Phragmites| No          | 68        | 92        | 92        | 143       | 150       |
| CCP1 | Calamagrostis | Phragmites| Yes        | 61        | 79        | 80        | 88        | 88        |
| CCP10| Calamagrostis| Phragmites| Yes        | 70        | 83        | 76        | 85        | 88        |
| CCP10CU| Calamagrostis | Phragmites| No         | 70        | 85        | 93        | 101       | 110       |
| CCP11 | Calamagrostis | Phragmites| Yes        | 79        | 97        | 106       | 112       | 120       |
| CCP11CU| Calamagrostis| Phragmites| No         | 80        | 100       | 104       | 111       | 111       |
| CCP12 | Calamagrostis | Phragmites| Yes        | 75        | 101       | 115       | 118       | 118       |
| CCP12CU| Calamagrostis | Phragmites| No         | 74        | 103       | 118       | 121       | 125       |
| CCP1CU | Calamagrostis | Phragmites| No         | 63        | 67        | 74        | 93        | 100       |
| CCP2 | Calamagrostis | Phragmites| Yes        | 67        | 81        | 93        | 110       | 145       |
| CCP2CU| Calamagrostis | Phragmites| No         | 67        | 87        | 95        | 98        | 110       |
| CCP3 | Calamagrostis | Phragmites| Yes        | 67        | 95        | 105       | 95        | 95        |
| CCP3CU| Calamagrostis | Phragmites| No         | 68        | 82        | 87        | 94        | 96        |
| CCP4 | Calamagrostis | Phragmites| Yes        | 70        | 90        | 99        | 110       | 118       |
| CCP4CU| Calamagrostis | Phragmites| No         | 71        | 93        | 91        | 202       | 115       |
| CCP5 | Calamagrostis | Phragmites| Yes        | 71        | 99        | 110       | 120       | 124       |
| CCP5CU| Calamagrostis | Phragmites| No         | 70        | 90        | 89        | 94        | 95        |
| CCP6 | Calamagrostis | Phragmites| Yes        | 65        | 104       | 74        | 98        | 100       |
| CCP6CU| Calamagrostis | Phragmites| No         | 64        | 86        | 91        | 99        | 105       |
| CCP7 | Calamagrostis | Phragmites| Yes        | 64        | 84        | 91        | 105       | 112       |
| CCP7CU| Calamagrostis | Phragmites| No         | 65        | 86        | 94        | 109       | 110       |
| CCP8 | Calamagrostis | Phragmites| Yes        | 62        | 86        | 96        | 90        | 90        |
| CCP8CU| Calamagrostis | Phragmites| No         | 59        | 96        | 107       | 124       | 130       |
| CCP9 | Calamagrostis | Phragmites| Yes        | 79        | 107       | 112       | 118       | 135       |
| CCP9CU| Calamagrostis | Phragmites| No         | 79        | 81        | 94        | 100       | 103       |
| PCA1 | Phragmites | Carex     | Yes         | 56        | 136       | 158       | 193       | 225       |
| PCA1CU| Phragmites | Carex     | No          | 54        | 107       | 120       | 130       | 148       |
| PCA2 | Phragmites | Carex     | Yes         | 53        | 89        | 112       | 142       | 170       |
| PCA2CU| Phragmites | Carex     | No          | 50        | 110       | 116       | 144       | 165       |
| PCA3 | Phragmites | Carex     | Yes         | 77        | 108       | 131       | 160       | 173       |
| PCA3CU| Phragmites | Carex     | No          | 76        | 129       | 149       | 174       | 175       |
| PCA4 | Phragmites | Carex     | Yes         | 85        | 159       | 200       | 210       | 220       |
| PCA4CU| Phragmites | Carex     | No          | 87        | 130       | 144       | 147       | 147       |
| PCA5 | Phragmites | Carex     | Yes         | 68        | 113       | 135       | 152       | 180       |
| PCA5CU| Phragmites | Carex     | No          | 70        | 137       | 154       | 187       | 188       |
| PCA6 | Phragmites | Carex     | Yes         | 58        | 117       | 134       | 159       | 162       |
| PCA6CU| Phragmites | Carex     | No          | 60        | 106       | 112       | 134       | 135       |
| PCC1 | Phragmites | Calamagrostis | Yes | 52        | 137       | 167       | 210       | 210       |
| PCC1CU| Phragmites | Calamagrostis | No | 49        | 108       | 125       | 147       | 150       |
| PCC2 | Phragmites | Calamagrostis | Yes | 51        | 126       | 163       | 205       | 219       |
Differences in above-ground resource acquisition and niche overlap

| ID      | Phytometer | Neighbour | Competition | 10-May-17 | 27-May-17 | 07-Jun-17 | 16-Jun-17 | 28-Jun-17 |
|---------|------------|-----------|-------------|-----------|-----------|-----------|-----------|-----------|
| PCC2CU  | Phragmites | Calamagrostis | No          | 54        | 140       | 180       | 217       | 240       |
| PCC3    | Phragmites | Calamagrostis | Yes         | 51        | 132       | 165       | 199       | 215       |
| PCC3CU  | Phragmites | Calamagrostis | No          | 50        | 79        | 100       | 124       | 230       |
| PCC4    | Phragmites | Calamagrostis | Yes         | 59        | 155       | 207       | 260       | 292       |
| PCC4CU  | Phragmites | Calamagrostis | No          | 57        | 136       | 176       | 210       | 220       |
| PCC5    | Phragmites | Calamagrostis | Yes         | 54        | 106       | 115       | 164       | 170       |
| PCC5CU  | Phragmites | Calamagrostis | No          | 55        | 113       | 150       | 174       | 185       |
| PCC6    | Phragmites | Calamagrostis | Yes         | 76        | 118       | 121       | 122       | 125       |
| PCC6CU  | Phragmites | Calamagrostis | No          | 78        | 129       | 148       | 166       | 180       |
| PTY1    | Phragmites | Typha | Yes         | 63        | 118       | 153       | 190       | 204       |
| PTY1CU  | Phragmites | Typha | No          | 64        | 133       | 165       | 194       | 209       |
| PTY2    | Phragmites | Typha | Yes         | 58        | 133       | 171       | 220       | 236       |
| PTY2CU  | Phragmites | Typha | No          | 56        | 129       | 165       | 170       | 210       |
| PTY3    | Phragmites | Typha | Yes         | 71        | 151       | 183       | 216       | 244       |
| PTY3CU  | Phragmites | Typha | No          | 70        | 134       | 156       | 196       | 222       |
| PTY4    | Phragmites | Typha | Yes         | 80        | 161       | 163       | 235       | 268       |
| PTY4CU  | Phragmites | Typha | No          | 84        | 163       | 198       | 233       | 264       |
| PTY5    | Phragmites | Typha | Yes         | 77        | 132       | 163       | 189       | 211       |
| PTY5CU  | Phragmites | Typha | No          | 75        | 144       | NC        | NC        | NC        |
| PTY6    | Phragmites | Typha | Yes         | 86        | 156       | 201       | 222       | 244       |
| PTY6CU  | Phragmites | Typha | No          | 88        | 146       | 175       | 220       | 238       |
| TYP1    | Typha     | Phragmites | Yes         | 85        | 182       | 223       | 252       | 252       |
| TYP1CU  | Typha     | Phragmites | No          | 84        | 153       | 194       | 230       | 248       |
| TYP2    | Typha     | Phragmites | Yes         | 76        | 150       | 200       | 255       | 263       |
| TYP2CU  | Typha     | Phragmites | No          | 74        | 158       | 102       | 244       | 270       |
| TYP3    | Typha     | Phragmites | Yes         | 84        | 170       | 207       | 252       | 288       |
| TYP3CU  | Typha     | Phragmites | No          | 82        | 167       | 192       | 229       | 268       |
| TYP4    | Typha     | Phragmites | Yes         | 87        | 173       | 118       | 267       | 284       |
| TYP4CU  | Typha     | Phragmites | No          | 89        | 174       | 217       | 247       | 274       |
| TYP5    | Typha     | Phragmites | Yes         | 76        | 179       | 218       | 276       | 302       |
| TYP5CU  | Typha     | Phragmites | No          | 76        | 144       | 186       | 210       | 244       |
| TYP6    | Typha     | Phragmites | Yes         | 70        | 162       | 187       | 249       | 288       |
| TYP6CU  | Typha     | Phragmites | No          | 72        | 157       | 190       | 245       | 270       |
Appendix D

Height of phytometers at establishment in 2016 (n = 96) and 2017 (n = 96). Phytometers were paired by height to account for natural variation among plants in the field.

Appendix E

Photosynthetic water use efficiency (mmol CO₂ mol⁻¹ H₂O) at varying levels of photosynthetically active radiation (μmol s⁻¹ m⁻²) for resident plant species (A) and *P. australis* phytometers (B) growing with or without above-ground competition. Error bars represent standard error.

Appendix F

Averages and standard errors for light compensation points (LCPT) (μmol photons m⁻² s⁻¹) and light saturation points (LSP) (μmol photons m⁻² s⁻¹) for each phytometer and treatment. All resident species grew with *P. australis* as neighbours, while *P. australis* phytometers grew with resident species as neighbours. A Carex phytometer growing without competition was removed from the data as an outlier as it had a LCPT value of 35.92 μmol photons m⁻² s⁻¹ and a LSP of 1,123,061.01 μmol photons m⁻² s⁻¹. There were nine instances where the non-linear least squares regression did not accurately model the data and so we have
omitted them and report the sample size of the remaining models (N).

Appendix G

ANOVA results for light compensation points (μmol photons m\(^{-2}\) s\(^{-1}\)) and light saturation points (μmol photons m\(^{-2}\) s\(^{-1}\)) with either resident species phytometers (C. aquatilis, C. canadensis, Typha spp.) and treatment (with competition or without competition) as fixed factors. *LCPT for P. australis growing with Carex was significantly higher than the LCPT of P. australis growing with Typha spp.

| Treatment                      | N   | LCPT         | LSP          |
|-------------------------------|-----|--------------|--------------|
| *Calamagrostis candensis*     |     |              |              |
| Without competition           | 19  | 23.7 (± 4.03)| 712.0 (± 147.0)|
| Competition                   | 24  | 23.6 (± 4.95)| 683.0 (± 63.6)|
| *Carex aquatilis*             |     |              |              |
| Without competition           | 13  | 38.0 (± 6.83)| 699.0 (± 46.7)|
| Competition                   | 13  | 29.7 (± 5.25)| 495.0 (± 50.1)|
| *Typha spp.*                  |     |              |              |
| Without competition           | 8   | -10.7 (± 27.3)| 832.0 (± 156)|
| Competition                   | 11  | 25.0 (± 9.27)| 556.0 (± 27.6)|
| *Phragmites australis* with *C. canadensis* |   |              |              |
| Without competition           | 12  | 35.9 (± 7.44)| 888.0 (± 80.1)|
| Competition                   | 12  | 17.6 (± 13.5)| 861.0 (± 86.5)|
| *Phragmites australis* with *C. aquatilis* | |              |              |
| Without competition           | 11  | 35.8 (± 5.18)| 855.0 (± 51.9)|
| Competition                   | 12  | 31.5 (± 6.87)| 748.0 (± 40.2)|
| *Phragmites australis* with *Typha* spp. | |              |              |
| Without competition           | 12  | 18.2 (± 7.52)| 835.0 (± 95.8)|
| Competition                   | 10  | -9.83 (± 18.5)| 980.0 (± 97.3)|
| Species | Competition | Spp × Treatment | Resid | Neighbours | Competition | Neighbour × Treatment | Resid |
|---------|-------------|-----------------|-------|------------|-------------|-----------------------|-------|
| LCPT    | 2 0.125 0.882 1 < 0.001 0.988 2 2.234 0.114 81 | 2 3.690 0.031* 1 1.390 0.243 2 0.558 0.575 63 |
| LSP     | 2 1.121 0.331 1 0.046 0.830 2 0.964 0.386 81 | 2 0.604 0.550 1 0.061 0.805 2 0.301 0.742 63 |

Differences in above-ground resource acquisition and niche overlap.
Appendix H

Light compensation points (μmol photons m$^{-2}$ s$^{-1}$) for resident phytometers (A) and *P. australis* phytometers (B), and light saturation point (μmol photons m$^{-2}$ s$^{-1}$) for resident phytometers (C) and *P. australis* phytometers (D) growing with or without competition. One outlier was removed from the plots—a *Carex* phytometer growing without competition which had a LCPT value of 35.92 μmol photons m$^{-2}$ s$^{-1}$ and a LSP of 1,123,061.01 μmol photons m$^{-2}$ s$^{-1}$. Boxplots represent the approximate 95% confidence intervals for comparing medians.
Appendix I

Light compensation points (μmol photons m$^{-2}$ s$^{-1}$) (A—C) and light saturation points (μmol photons m$^{-2}$ s$^{-1}$) (D—F) for resident phytometers (with and without competition) compared to P. australis growing adjacent to that specific resident species (also with and without competition). One outlier was removed from the plots—a Carex phytometer growing without competition which was estimated to have a LCPT value of 35.92 μmol photons m$^{-2}$ s$^{-1}$ and a LSP of 1,123,061.01 μmol photons m$^{-2}$ s$^{-1}$. Boxplots represent the approximate 95% confidence intervals for comparing medians. Because values could be affected by environmental conditions that differ among habitats occupied by the different resident species, t-test results compare the values from resident species exclusively to values from P. australis phytometers growing adjacent to that resident species.
Appendix J

The percent of photosynthetically active radiation reaching the top of each phytometer growing with or without competition (A) and the total aboveground biomass produced by each species growing with or without competition (B). Large symbols represent the average and error bars represent standard error.
Appendix K

The growth of phytometers over the 2016 (A) and 2017 (B) growing seasons. Resident species represent remnant emergent marsh (*Typha* spp.), sedge meadow (*Carex aquatilis*) and meadow marsh (*Calamagrostis canadensis*) growing with or without above-ground competition from *P. australis*, while invasive *P. australis* grew with or without above-ground competition from resident species. Note that we took the height measures as a proxy for aboveground biomass approximately every 10 days from the start of the experiment until two weeks before we terminated the experiment and harvested phytometers for biomass. Error bars represent standard error.

Appendix L

Eigenvalue and variance explained by the first three axes of our PCA, and the eigenvector values of all environmental variables included in the analysis.
Appendix M

The scree plot assessing inertia of the environmental variable PCA. Axes PC1 and PC2 were selected for further analyses.
Appendix N

Projections of the 95% niche regions for each plant species based on weighted PCA axis scores (A); quadrats include one-dimensional density plots and 10 randomly drawn ellipses per species which represent the two-dimensional niche region (A). Posterior distribution of the probabilistic niche overlap metric (%) for specified 95% niche region of all four plant species. Plots show the overlap probability of species A (row) onto the niche of species B (column). The posterior means and 95% credible intervals are displayed in black.

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