Long-term Effects of a Phragmites australis *Invasion on Birds in a Lake Erie Coastal Marsh*

by

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Author's declaration

I hereby declare that I am the soul author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Invasive *Phragmites australis* threatens the integrity of essential bird habitat in coastal marshes. Located on the north shore of Lake Erie, Long Point, Ontario provides habitat to thousands of breeding and migrating birds, including marsh-nesting species in decline around the Great Lakes. Invasive *P. australis* has been colonizing these marshes since the late 1990s, when concerns prompted a survey of birds in invaded wetlands (2001-2002). My work evaluates birds in these wetlands after over a decade of *P. australis* expansion, comparing birds among *P. australis* and the vegetation communities it is displacing: cattail marsh, meadow marsh, and open-water marsh. I also examined bird community composition and functional traits to better capture the effects of *P. australis* invasion. I observed substantial changes since the 2001-2002 study was conducted. In 2015, total bird abundance was lower in *P. australis* than cattail marsh, with little difference in bird species richness among vegetation types. Bird community composition was distinct among all four vegetation types; however, *P. australis* supported a subset of bird species within cattail and meadow marsh habitat, rather than novel bird species. *Phragmites* habitat excludes many marsh-nesting species and provides habitat for shrub-nesting, foliage gleaner bird species. Marsh-nesters of conservation concern are restricted to remaining cattail and meadow marsh, and open-water habitat. My work indicates that the full effects of *P. australis* invasion may exhibit a lag time, and that community composition and functional traits should be considered when evaluating the effects of a biological invasion.

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1.0 Literature review and thesis scope

The introduced aquatic grass *Phragmites australis* (Cav.) Trin. ex Steud (European common reed; *P. australis* hereafter) is rapidly spreading throughout North American wetlands. The tall, dense stands created by this aggressive invader alter wetlands by reducing light availability, filling in areas of open-water, negatively impacting floral diversity, and increasing litter accretion rates (Able et al., 2003; Hirtreiter and Potts, 2012; Keller, 2000; Rooth et al., 2003). *Phragmites australis* invasion is changing the coastal marshes of Long Point, ON, where more than 70% of the total wetland area on the north shore of Lake Erie is found (Ball et al., 2003). In addition to being a critical staging ground for both the Mississippi and Atlantic Flyways, Long Point provides essential habitat to a number of bird species that rely on marshes for breeding (Bird Studies Canada, 2016). The expansion of *P. australis* in Long Point in the late 1990s led to the displacement of historical resident meadow marsh and cattail marsh (Wilcox et al., 2003), changing these coastal habitats with potential consequences for the birds that rely on them. In my thesis, I evaluate the effect of the *P. australis* invasion in Long Point on bird communities. This literature provides background information in support of that aim, namely I review the history of *P. australis* invasion in Canada and evaluate the state of our knowledge of *P. australis* biology and its effects on invaded ecosystems, with special reference to potential direct and indirect effects on waterbirds.

1.1 Invasion biology

The introduction of a non-native species into a new environment can have far-reaching consequences for the resident species, biological communities, and ecological functions of an invaded system (Cadotte et al., 2006; Vilà et al., 2011). Introduced plants have been shown to

have bottom-up effects on higher trophic levels, and reduce resident plant species diversity (Vilà et al., 2011). In the United States, introduced species pose a significant risk to threatened or endangered species and have been estimated to cost the country $120 billion a year in environmental damages and losses (Pimentel et al., 2005). In Canada, of the 488 species categorized as at risk in 2006, 22% were considered most severely threatened by introduced species (Venter et al. 2006). While the consequences of introduced species are serious, many non-native species introduced to new ecosystems fail to overcome the many abiotic and biotic barriers to become invasive (Mack et al., 2000). Biological invasions, for conceptual clarity, are commonly described as occurring in a series of non-discrete stages: transport/introduction, colonization, establishment, and spread (Fig. 1-1) (Davis, 2009; Theoharides and Dukes, 2007; Vermeij, 1996). A species that can form reproducing populations in a new range is considered introduced, or naturalized, but only once this species spreads outside of its introduced range is it considered invasive (Richardson et al. 2000b).

The first stage of invasion, transport, involves movement over a geographic barrier, usually facilitated by human activities. For a species to successfully reach a new range there must be multiple opportunities for propagules to survive transport and reach a new environment, otherwise known as high propagule pressure (Lockwood et al., 2005; Richardson et al., 2000a,b). Propagule pressure is a measurement of the number of individuals released into new area, and includes a measure of both the number of individuals released in any one event and the number of release events (Lockwood et al., 2005). During the transport stage, the more abundant the propagules reaching the new area, the greater the likelihood of successful transport (Theoharides and Dukes, 2007). Furthermore, species with a large native range that experience multiple

successful introductions may exhibit higher genetic diversity in their new range, helping the species escape genetic bottlenecks in their introduced range (Theoharides and Dukes, 2007).

The second stage is colonization. For a plant to successfully colonize a new environment – survive the transport stage and begin to grow in the new area – there are a number of abiotic factors to overcome. While climate is a coarse filter for many introduced species, the availability of light, nutrients, and moisture can also determine if an introduced species will be successful (Theoharides and Dukes, 2007). Disturbance that removes resident vegetation and adds nutrients can increase the probability of transport leading to successful colonization (Leishman and Thomson, 2005; Minchinton and Bertness, 2003). High propagule pressure is also a factor in colonization success, as this can rescue small introduced populations from extinction by providing a constant addition of viable propagules to the area (Theoharides and Dukes, 2007). If the introduced species has colonized a site and is able to reproduce, creating a self-sustaining population without any anthropogenic assistance, the invasion progresses to the third stage: establishment (Theoharides and Dukes, 2007).

Establishment requires that the introduced plant species to be able to tolerate the abiotic factors of the new range, and overcome limitations from biotic interactions (Theoharides and Dukes, 2007). During this stage, a species must be able to access resources that are adequate for growth, maintenance and reproduction, find gametes for out-crossing, and survive long enough to reproduce (Davis, 2009). If the population is self-sustaining in its introduce range it can be considered "naturalized" (Richardson et al., 2000b). In this stage, invasive species benefit from traits that enhance competitive performance (fast growth, allelopathy) and reduce niche overlap with resident plants (Theoharides and Dukes, 2007). Interactions other than competition also contribute to the success of introduced species. The enemy-escape hypothesis, i.e., the transport

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of the introduced species outside of its enemies' range, (e.g. Wolfe, 2002), has been suggested to benefit introduced species in their new range. With less herbivore or predator pressure, introduced species may allocate more energy to growth rather than defenses (Blossey and Notzold, 1995). In direct regards to reproduction, species that can reproduce vegetatively or do not rely on pollinators may have an advantage during establishment (Richardson et al., 2000a; Theoharides and Dukes, 2007).

To be considered "invasive" a species must persist and expand its distribution outside of its introduced range. This leads to the next stage of invasion, "spread", which can involve both a gradual increase in spatial cover and new populations arising from dispersal from the original colonization sites (Davis, 2009; Theoharides and Dukes, 2007). Human activities are central to the spread stage. Habitat fragmentation by humans can facilitate the spread stage of invasion, resulting in high concentrations of introduced species along habitat edges (Theoharides and Dukes, 2007). Disturbances, such as transportation routes, that result in more edge habitat, pathways connecting different habitat, and the removal of resident plant communities and addition of nutrients provide ample opportunity to invasive species to spread.

While many species are introduced into new ranges, few are able to overcome the limitations of new environments. Those that do, and are capable of creating reproducing populations that spread outside of their introduced range, can have a number of effects on resident ecosystems, changing community interactions, altering habitats, and affecting biodiversity. The stages of invasion provide a conceptual model for framing the spatial and temporal differences in invasion progression (Fig. 1-1). Likely, when examining the effects of a biological invasion on a certain community, there will be differences in the community's response over these various stages.

1.2 History of invasion by Phragmites australis

The first record of introduced *P. australis* in Canada is from 1910 in Nova Scotia, and by the 1920s it had reached the St. Lawrence River, near Quebec City (Catling and Mitrow, 2011). By 1950, it was observed only in four areas within Canada, compared to the native lineage's widespread distribution (Catling and Mitrow, 2011). Within Quebec, the introduced lineage was rare until the 1970s, when it began to spread inland facilitated by the development of transportation networks (Lelong et al., 2007). By 1990, introduced *P. australis* had spread throughout the St. Lawrence and Southern Ontario (Catling and Mitrow, 2011) and became a dominant wetland species in many marshes (Lelong et al., 2007). Introduced *P. australis* is now spreading further west, into northern Ontario, southern Manitoba, and southern British Columbia, and is expected to become established across most of southern Canada (Catling and Mitrow, 2011).

1.3 Phragmites australis *biology*

1.3.1 Introduced Phragmites australis

The genus *Phragmites* currently includes four species: *Phragmites australis* (Cav.) Trin. Ex Steud, *Phragmites japonicas* Steud., *Phragmites karka* (Retz.) Trin. Ex Steud., and *Phragmites mauritianus* Kunth (Saltonstall, 2016; WCSP, 2015), of which only *Phragmites australis* has a global distribution (Saltonstall, 2016). The taxonomy of *P. australis* is out of date, though there has been extensive research into the species in North America. What does remain clear is there are three lineages of *P. australis* in North America: a native lineage, previously designated as *P. australis* ssp. a*mericanus* (Saltonstall, P.M. Peterson, & Soreng), a Gulf Coast lineage, *P. australis* var. *berlandieri* (E. Fourn.) Saltonstall & Hauber, and an introduced lineage. The

introduced lineage is differentiated based on morphological characteristics and chloroplast DNA markers. Evidence suggests that the introduced lineage is quite diverse relative to the native lineage (Plut et al., 2011). Haplotype M is the most widespread haplotype from the introduced lineage, and most likely originates in the UK (Plut et al., 2011). The high genetic diversity in the introduced lineage is interpreted as evidence of multiple introduction events and a high propagule pressure from the genetically diverse European range of *P. australis* (Plut et al., 2011). This is supported by the recent discovery of a second haplotype of introduced *P. australis*, haplotype L1, in Quebec (Meyerson and Cronin, 2013). In addition, some of the genetic variation observed in the introduced *P. australis* is due to transmission of chloroplast DNA through pollen (paternal leakage), resulting in novel haplotypes that experts believe arose in North America (Lambertini, 2016). As a consequence of these recent discoveries, the taxonomy of *P. australis* is in flux. Currently, the introduced and native lineages of *P. australis* are treated as different subspecies by certain authors (e.g. Bhattarai et al. 2016; Saltonstall et al. 2016) although the integrated taxonomic information system considers *P. australis* ssp. a*mericanus* and ssp. *australis* to be synonymous. For clarity in this document, any reference to *P. australis* will mean the introduced lineage, unless otherwise specified.

1.3.2 Native vs Introduced Phragmites australis

Gene flow between introduced *P. australis* and native *P. australis* is low, even where there is geographical overlap between multiple lineages (Saltonstall, 2003b; Saltonstall et al., 2010), though instances of hybridization have recently been observed (Meyerson et al., 2012; Saltonstall et al., 2016, 2014). Introduced *P. australis* exhibits more aggressive growth and establishment characteristics than its native counterpart. Introduced *P. australis* shoots emerge earlier in the

growing season, produce double the total and leaf biomass, and transition faster from buds to root or shoot tissues (League et al., 2006). Compared with the native lineage, introduced *P. australis* has a 38 – 83% larger photosynthetic canopy, higher specific leaf area, and maintains a 51% greater photosynthetic rate (Mozdzer and Zieman, 2010). Patches of introduced *P. australis* are also denser and taller than the native lineage. A comparison between native *P. australis* and introduced *P. australis* in coastal and inland wetlands near Lake Michigan found that introduced *P. australis* exhibited greater stem densities (31.9 stems per m^2) than the native lineage (22.3 stems per m^2), and reached a higher maximum height (306 cm) than the native lineage (246 cm) (Price et al., 2014). While the native lineage does produces patches that can be quite tall and dense, the diversity and species composition of vegetation communities associated with native *P. australis* were similar to uninvaded communities, while vegetation associated with introduced *P. australis* had low diversity and supported more generalist species (Price et al., 2014). This suggests that the height and density characteristics alone of *P. australis* cannot fully account for its success as an invader.

The differences in lineages are also manifested in rhizome structure. The rhizomes of introduced *P. australis* are larger than native rhizomes. The diameters of native rhizomes are less than 15 mm, while introduced rhizomes are flatter and greater than 15 mm in diameter (Mal and Narine, 2004). Introduced *P. australis* allocates 60 – 70% of its total biomass to roots and rhizomes (Mal and Narine, 2004; Shay and Shay, 1986), creating extensive networks that capture soil nutrients. Rhizomes can mobilize resources and allocate them to younger, smaller shoots during the early growing stage to achieve a more uniform final stand structure (Hara et al., 1993). This clonal subsidy provides a boost to *P. australis* and enhances the growth of young, uneven aged stands (Hara et al., 1993). These above- and below-ground structures maximize

resource consumption for *P. australis*, improving competitive ability, but they are not the only factor that allows the introduced lineage to be so prolific. The introduced lineage is also more responsive to disturbances and increases in nutrient availability, an attribute which has been linked to its successful invasion of disturbed wetlands where nutrient pollution is a common result of human activities (Minchinton and Bertness, 2003).

1.4 Environmental tolerances and response to disturbance

1.4.1 Water depth and salinity tolerances

In addition to aggressive growth characteristics, introduced *P. australis* can tolerate a broad range of environmental conditions and hazards. Introduced *P. australis* can grow in a wide range of water depths, from areas where the water table is a meter below the soil surface to standing water greater than 50 cm deep (Shay and Shay, 1986). Experiments growing *P. australis* in variable water depths, reaching up to 230 cm, have revealed developmental plasticity in *P. australis* which allows it to adapt its morphology to different water depths (Engloner and Papp, 2006; Vretare et al., 2001). In deep water, 70 – 75 cm, *P. australis* allocates less biomass below-ground and makes fewer, taller shoots which serve to increase gas exchange but can make the plant more vulnerable to wave action (Vretare et al., 2001). This may be the reason that introduced *P. australis* in natural settings seems limited to water depths less than 100 cm and its growth is restricted under prolonged flooding (> 100 days) (Hudon et al., 2005; Shay and Shay, 1986).

Introduced *P. australis* is also tolerant to a range of salinities and able to grow in freshwater, brackish, and salt marshes (Konisky and Burdick, 2004). Introduced *P. australis* has higher relative growth rates and is capable of producing more shoots in saline and freshwater

environments than the native lineage, and can maintain half of its growth potential at 0.4 M NaCl, while native lineages cannot grow above 0.1 M NaCl (Vasquez et al., 2005). The ability of introduced *P. australis* to survive fluctuating water levels and salinity levels may explain why it is so often observed in road side ditches, where de-icing salt is often applied (Jodoin et al., 2008). Certainly, the capacity to tolerate a wide range of environmental conditions would facilitate invasion into new habitats.

1.4.2 Response to herbivory

The predator escape hypothesis is commonly called upon to explain the success of an invading species (e.g., Wolfe, 2002), and in the case of introduced *P. australis* it seems plausible that reduced grazing and infection may contribute to the success of the introduced lineages. Introduced *P. australis* also appears to have a higher resistance to pests and herbivores than the native lineage. Aphid *(Aphididae)* densities were significantly lower on non-native plants, while native *P. australis* was extensively fed on or even killed (Lambert and Casagrande, 2007). Lambert et al. 2007 focused on gall flies (*Lipara* sp.) in *P. australis* and found that, when stands were adjacent to each other, introduced *P. australis* was colonized less than native plants, which did not flower when they were infected (Lambert et al., 2007). In other field and common greenhouse comparisons, native *P. australis* experienced significantly higher aphid densities and gallfly damage to leaves and stems than introduced *P. australis* (Park and Blossey, 2008).

The co-evolutionary history of introduced *P. australis* has also been suggested as a reason it may experience less herbivory pressure in North America. Native *P. australis* has co-evolved with fewer than 10 herbivore species, while in Europe introduced *P. australis* evolved with over 100 herbivores (Tewksbury et al., 2002). In North America, the current assemblage of

herbivores feeding on both introduced and native *P. australis* is mostly comprised of introduced

European species, leading researchers to hypothesize that introduced *P. australis* experiences

lower predation because of its co-evolutionary history (Park and Blossey, 2008; Tewksbury et

al., 2002). However, there is on-going debate in the literature about whether herbivores really are

haplotype-specific and the implications for biological control of *P. australis.* Some argue that

certain species of insects are specific in consuming the introduced haplotype, and pose minimal

threats to native plant species (Blossey and Casagrande, 2016a, 2016b), while others believe that

the predation is not specific enough and it poses a risk to non-target plants (Bhattarai et al.,

2016). Hence, the potential of biocontrol agents to assist in *P. australis* control remains hotly

contested and requires additional study.

1.4.3 Response to disturbance

Anthropogenic and natural disturbances create canopy gaps or empty niches that

represent opportunities for *P. australis* invasion, as the introduced lineage is opportunistic and

tolerant of disturbance. Once a gap is created, its rapid growth rate and ability to reproduce

vegetatively (see below) help *P. australis* become established (Zedler and Kercher, 2004).

Phragmites australis density is positively associated with the percent of surrounding developed

land (Hughes et al., 2016), and in newly invaded areas the introduced lineage was found most

frequently in areas with urban disturbance near wetlands (Lambert et al., 2016). In Chesapeake

Bay, the prevalence of agriculture was a strong predictor of *P. australis* invasion at regional and

local scales (Sciance et al., 2016). Experimental manipulation mimicking shoreline disturbance

via vegetation removal and nutrient addition increased the cover, density, and height of

introduced *P. australis*, as well as the distance shoots spread laterally (Minchinton and Bertness,

2003). Introduced *P. australis* excels at proliferating in disturbed areas, capitalizing on the exposed substrate and nutrient additions typically associated with urban and agricultural development.

In addition to anthropogenic disturbances, natural disturbances such as storms allow *P. australis* to proliferate. For example, the high rates of precipitation during an El Niño year led to *P. australis* producing 30% more shoots, which were 25% taller and had significantly more inflorescences than the year before in coastal brackish marshes of southern New England (Minchinton, 2002). Similarly, the natural drawdown of Lake Erie in the 1990s is thought to be responsible for the rapid expansion of introduced *P. australis*, as reported by Wilcox (2012). Thus, *P. australis* benefits from its wide tolerance environmental conditions and its ability to take advantage of nutrient pollution and physical disturbance through rapid growth and canopy closure.

1.5 Life span

Although the ramets or above ground portions of *P. australis* plants senesce every fall, the rhizomes of *P. australis* are perennial and because of its clonal growth form, individuals may live a long time. There is not an abundance of data on *P. australis* life span, but some research suggests that a single clone of *P. australis* can maintain itself for hundreds of years (Haslam, 1972). *Phragmites australis* can reproduce both vegetatively, via rhizomes or stolons, and sexually, via seeds. The rhizomes of *P. australis* live approximately 3-7 years (Mal and Narine, 2004), and buds emerge in April or May, reach their final height in late August, and flower 4 – 5 months after emergence (Haslam, 1970a). Introduced *P. australis* has an extended growing season relative to the native lineage, and does not begin senescing until September or October

(Mozdzer and Zieman, 2010). The length of the growing season may provide introduced *P. australis* with more opportunity for nutrient uptake and carbohydrate synthesis, contributing to its success as an invader (Zedler and Kercher, 2004).

1.6 Reproduction

1.6.1 Sexual reproduction

Phragmites australis is able to reproduce both sexually and asexually which allows it to spread widely, colonize new areas, and maintain high genetic diversity while also establishing stands of locally adapted clones, well suited to surrounding environmental conditions (Kettenring et al., 2016). Sexual reproduction in *P. australis* is not considered its primary reproductive strategy, but there is mounting evidence that reproduction via seeds is essential for colonizing new areas (Belzile et al., 2010; Kettenring et al., 2016; Kettenring and Mock, 2012). Seed dispersal and sexual reproduction appears to be more common in the introduced lineage than the native and potentially offer more opportunities for seedling establishment (Kettenring and Mock, 2012). In populations of *P. australis* that have been examined for genetic relatedness, there is usually a great deal of genetic diversity that is indicative of seeds as a primary reproductive propagule (Belzile et al., 2010; Stabile et al., 2016). The seeds of *P. australis* mature at the end of its growing season, from September to October, and it can take years after sprouting for flowering shoots to emerge (Ishii and Kadono, 2002; Saltonstall et al., 2010).

Phragmites australis is also capable of self-fertilization, and the large flowers of the introduced lineage, larger than native *P. australis*, produce a great amount of highly fertile, wind-dispersed pollen (Lambert and Casagrande, 2007; Saltonstall et al., 2010). The ability to self-pollinate provides an advantage during the colonization stage of invasion, allowing *P.*

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australis to bypass biotic limitations in new environments (Richardson et al., 2000a; Theoharides and Dukes, 2007). Self-pollination may also give *P. australis* the opportunity to move into regions with poor pollen availability, and to expand further in areas where the plant is already established (Lambert and Casagrande, 2007).

The longevity of seeds in North American wetlands is not well understood (Baldwin et al., 2010), but field observations suggest seeds may persist for over a decade. As evidence of longevity, the expansion of *P. australis* in the Great Lakes region in the 1990s is attributed to *P. australis* inoculating the seedbank during previous low water levels of the 1980s (Wilcox, 2012). Germination and establishment of *P. australis* is closely tied to water levels. For establishment, seeds require wet soil that is not flooded above 1 cm, contains high nutrients, and has an open canopy (Haslam, 1971a). Early germination and establishment is important for *P. australis* seedling survival, as it allows shoots time to emerge above water and reach the light (Weisner and Ekstam, 1993). Long term inundation of seedlings will result in decreased survival, and this effect is enhanced by the presence of algae that can further hamper photosynthesis (Armstrong et al., 1999). While flooding can kill seedlings, they are also susceptible to drying if too exposed and to competition with established plants (Haslam, 1972).

1.6.2 Vegetative reproduction, spread, and patch dynamics

Phragmites australis patches can become established by either seeds or vegetative propagules, but their aggressive lateral spread is facilitated by rhizomes and above-ground stems (Mal and Narine, 2004). *Phragmites australis* can spread by colonization, linear clonal growth, or circular clonal growth of patches, and within invaded wetlands patch numbers increase over time before decreasing as large patches integrate with one another (Lathrop et al., 2003). Lateral

expansion of patches is enhanced by stolons, which can arise from fallen stems or horizontal rhizomes (Appendix 1c) (Brisson et al., 2010). *Phragmites australis* relies heavily on these means of vegetative reproduction. Rhizomes in particular are capable of growing 2 m in one year and are an effective way to expand the population size as fragments as small as 10 – 20 cm can produce a new plant (Appendix 1a,b) (Juneau and Tarasoff, 2013). The rhizomes of *P. australis* are resilient to a number of stressors and are able to withstand temperature lows of -20 $^{\circ}$C, fire, disease, predators, and water stress (Mal and Narine, 2004), allowing them to disperse large distances. Vegetative growth also allows *P. australis* to expand into areas with deeper water than seeds could germinate in (Amsberry et al., 2000).

The structure of *P. australis* below-ground tissues consists of a main vertical rhizome growing from a horizontal rhizome that terminates in a shoot (Appendix 1b) (Haslam, 1970b). These horizontal rhizomes are responsible for renewing and maintaining the population – without them the vertical rhizomes become reduced in size until they die (Haslam, 1969). In the fall, *P. australis* resources are translocated from above-ground tissue into rhizomes, and are allocated to new growth in the spring (Juneau and Tarasoff, 2013). The primary storage carbohydrate is starch (Mal and Narine, 2004), which comprises 1 – 10% of above-ground biomass and 5 – 20% is stored in below-ground biomass (Wersal et al., 2013). Rhizomes that undergo overwintering receive carbohydrates from shoots to encourage growth when the growing season returns (Boar, 1996; Wersal et al., 2013), and it follows that rhizomes collected for greenhouse experiments in the fall have higher survivorship than those collected in the spring (Juneau and Tarasoff, 2013). Rhizomes allow *P. australis* to allocate resources to young shoots to achieve a stand structure with more uniform shoot height and weight (Hara et al., 1993). This clonal subsidy provides a boost to shoots that may be growing in less optimal conditions.

1.7 Spread vectors

The introduction of *P. australis* into North American in the 1990s most likely occurred at shipping ports where *P. australis* was transported from Europe in ship ballasts, and potentially used to fill in marshes that were later converted to railways or shipping ports (Lavoie et al., 2003; Saltonstall, 2002). A number of pathways have facilitated *P. australis* spread throughout North America, but the most predominant are transportation routes, including roads, railways, or shipping routes which create pathways between habitat ideal for colonization (Brisson et al., 2010). *Phragmites australis* was found around the St. Lawrence River in the 1960s and 70s, and the construction of transportation routes and agricultural drainage in this area provided ample opportunities for spread (Kettenring et al., 2012).

Roadways are a major contributor to *P. australis* spread as they create a network between suitable habitat, and *P. australis* can withstand increased salinity from sources such as de-icing salt while less salt tolerant species may be excluded (Brisson et al., 2010; Jodoin et al., 2008; Maheu-Giroux and de Blois, 2007; Zedler and Kercher, 2004). Heavy machinery, such as construction equipment, can transport rhizome fragments along roadways (Saltonstall et al., 2010), and invasion is common in disturbed habitat near roads. Introduced *P. australis* is abundant within wetlands that border roadways (Jodoin et al., 2008) and man-made wetlands near roads are more likely to be invaded than riparian habitats further from roads (Maheu-Giroux and de Blois, 2005). Seasonal flooding events may move rhizome propagules to new areas, and some research suggests that long distance dispersal occurs via waterways while short distance dispersal is over land (Kirk et al., 2011; Lavoie et al., 2003; Saltonstall et al., 2010). Genetic relatedness between stands declines with increasing distance, but *P. australis* appears to be able to disperse up to 500 m from an area (McCormick et al., 2016).

1.8 Study system

1.8.1 Current distribution in the Great Lakes

Water level fluctuation can change vegetation composition and assist invasions, as exemplified among Great Lakes coastal wetlands (Wilcox, 2012). Emergent vegetation cover increases during low water levels, a trend observed in both Lake Erie and Lake Michigan where *P. australis* cover expanded after a water level drop (Tulbure et al., 2007; Whyte et al., 2008). In the late 1980s introduced *P. australis* was not a dominant plant species in the Great Lakes – at this time *Typha* was the dominant plant species and the main concern towards Great Lake biodiversity (Keddy and Reznicek, 1986).

Tulbure and Johnston (2010) assessed the distribution of *P. australis* throughout the Great Lakes and noted that *P. australis* invasion was greater in Lakes Michigan, Huron and Erie, all of which experienced water level decreases between 1999 and 2001, while Lake Ontario, which experienced higher water levels between 1999 and 2001, had less *P. australis*. A 2007 study of Great Lakes coastal wetlands revealed that exotic plants were more prevalent in wetlands in Lake Erie and Ontario, intermediate in Lake Michigan, and lowest in Lakes Superior and Huron, but *P. australis* was present in all of the Great Lakes and was typically the dominant plant species (Trebitz and Taylor 2007). The presence of *P. australis* in the lower Great Lakes seems to be related to the amount of agriculture in the surrounding landscape, though the relationship may also be driven by other anthropogenic disturbances such as pollution (Trebitz and Taylor 2007).

1.8.2 Status in Long Point

Phragmites australis is identifiable in aerial photos of Long Point dating back to 1945 in small

amounts (4 ha to 17 ha), but it expanded from 18 ha to 137 ha between 1995 and 1999 (Wilcox

et al., 2003). The low water levels in Lake Erie during the mid-1980s likely provided a chance

for *P. australis* to inoculate exposed soil, and to emerge during the next low (Tulbure and

Johnston, 2010; Whyte et al., 2008; Wilcox et al., 2003). Of the *P. australis* population in Long

Point examined by Wilcox et al. (2003), 90% of the stands were haplotype M, and *P. australis*

mostly displaced resident *Typha* spp. (34%) and marsh meadow (31%) in the expansion between

1995 and 1999. More current mapping initiatives are underway in Long Point (Appendix 2), but

little has been done since 2002 in terms of *P. australis* management and research from McMaster

indicates that *P. australis* is still rapidly expanding throughout Long Point (Marcaccio and

Chow-Fraser, 2016).

1.8.3 Long Point study area

Located in the Carolinian zone of southern Ontario, Long Point is a 35 km sandspit that extends

into Lake Erie, containing 13,465 ha of wetlands and accounting for 70% of the total wetland

area on the north shore of Lake Erie (Ball et al., 2003). The spit contains a number of

ecologically significant zones and surrounds the Long Point inner bay, a 78 km^2 body of water

partially separated and protected from the wave action of Lake Erie (Meyer, 2003; UNESCO,

2015). On the Long Point sandspit, the undulating ridges create distinct plant communities

ranging from dunes on the southern beach, to wet sedge meadow, to Cottonwood savanna

(Reznicek and Catling, 1989). The differences in elevation along the sandspit also contribute to a

mosaic of habitats with ponds, meadows, and marshes occurring throughout Long Point

(Reznicek and Catling, 1989). Many of these vegetation zones are important for maintaining plant diversity and abundance as Long Point supports rare coastal marsh meadow habitat and a number of provincially rare plant species, many of which are wetland or aquatic species (Ball et al., 2003; Prince et al., 1992; Reznicek and Catling, 1989).

In addition to supporting diverse and significant vegetation communities, Long Point is an important area for avifauna. Located on the Atlantic flyway, the abundant submerged aquatic vegetation and protected waters of the bay and marsh complexes make Long Point a waterfowl staging area of international importance (Knapton and Petrie, 1999; Prince et al., 1992). Many migratory song birds also use Long Point as a stop-over, and several provincially significant bird species such as Bald Eagle *(Haliaeetus leucocephalus)*, Least Bittern *(Ixobrychus exilis)*, Great Egret *(Ardea alba)*, and Black Tern *(Chlidonias niger)* nest and feed in or near the coastal marshes (Ball et al., 2003). The regional and international importance of Long Point has been recognized through designations as a UNESCO World Biosphere Reserve, a RAMSAR wetland of international significance, and an Important Bird Area.

The significance of Long Point is evident when the context of the surrounding landscape is considered. Southern Ontario has experienced a substantial loss of wetlands since pre-settlement time: 72% in total, and an estimated loss of 3.5% per year since 1982, equivalent to 3,543 ha per year (Ducks Unlimited Canada, 2010). Haldimand-Norfolk, the county Long Point is in, has lost 65 – 85% of its wetland area since pre-settlement time (Ducks Unlimited Canada, 2010). This significant loss of wetland habitat in Haldimand-Norfolk emphasizes the ecological importance of Long Point for marsh dependent species in the region.

1.9 Effects of invasion

1.9.1 Effects on birds

My thesis is primarily concerned with the effects of *P. australis* invasion on birds, and so I will begin this section with a review of the conflicting evidence on how sensitive bird communities are to *P. australis* invasion. The changes that occur in wetlands when *P. australis* invades can affect birds that use these habitats directly and indirectly, though there is no consensus on what these effects are.

Early work in salt and brackish marshes found a decrease in bird species richness in *P. australis* habitat compared with short grass meadow and brackish mixture (emergent and short graminoid mix) (Benoit and Askins, 1999). Additionally, the bird species found within *P. australis* were present across all marsh habitat while state-listed species were confined to either short grass meadow, brackish mixture, or both (Benoit and Askins, 1999). Short-grass meadows were dominated by salt marsh specialists and generalists, while Marsh Wren (*Cistothorus palustris*), Red-winged Blackbird (*Agelaius phoeniceus*), and Swamp Sparrow (*Melospiza georgiana*) were most abundant in *P. australis* (Benoit and Askins, 1999). More recent work in tidal marshes along the Hudson Bay Estuary also found that *P. australis* invasion decreased bird species richness, changing the marshes from a diverse bird community to one dominated by Red-winged Blackbirds (Wells et al., 2008). In Lake Erie coastal marshes located in Ohio, *P. australis* patches supported the highest bird abundance but lowest species diversity when compared with floating-leaved, cattail, and mixed emergent habitat, but the observed increase in bird abundance was attributed to large roosts of Red-winged Blackbird using *P. australis* (Whyte et al., 2015). Tall, large patches of *P. australis* are considered low quality breeding habitat because of their closed canopy and dense stems, and increases in *P. australis* cover are predicted

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to decrease available roosting area for large-bodied birds such as Sandhill Crane *(Grus canadensis)* (Kessler et al., 2011); however, this decrease in roosting habitat may be offset by an increase in preferred hunting habitat as there is some evidence that larger-bodied birds use the edges of stands as feeding grounds (Benoit and Askins, 1999).

In contrast to the evidence that bird diversity is negatively affected by *P. australis* invasion, at least in the interior of *P. australis* stands, two studies from Long Point, ON suggest that *P. australis* may actually be beneficial to birds. In 2001-2002, a study comparing bird abundance and diversity between *P. australis,* cattail, and meadow marsh habitat found that *P. australis* supported a significantly higher total bird abundance and species richness, with these effects most strongly exhibited along the edge of *P. australis* habitat (Meyer et al., 2010). The bird communities within *P. australis* had higher abundances of Common Yellowthroat (*Geothlypis trichas*), Swamp Sparrow, Eastern Kingbird (*Tyrannus tyrannus*), Willow Flycatcher (*Empidonax traillii*), and Yellow Warbler (*Dendroica petechia*) (Meyer et al., 2010). There were no differences between the invaded and uninvaded marsh types in terms of marsh-nesting bird richness, though 25% more marsh-nesting individuals were observed in meadow marsh than *P. australis* (Meyer et al., 2010). In another Long Point study, researchers compared bird abundance and richness within natural ponds, dredged ponds, and mixed cattail- *P. australis* emergent vegetation and found that ponds supported greater total species richness and marsh-nesting species richness than cattail- *P. australis* habitat (Schummer et al., 2012). These researchers agreed with Meyer et al. (2010), and concluded that dredging ponds led to an increase in bird richness and abundance due to the creation of more edge habitat (Schummer et al., 2012).

A study by Gagnon Lupien et al. (2015) examining the effects of *P. australis* invasion on birds concluded that invasion had minimal effects. In recently invaded marshes in Quebec, *P. australis* did not appear to have any substantial effect on the richness, abundance, or diversity of songbirds or waterbirds using the marsh (Gagnon Lupien et al., 2015). Furthermore, species of concern including Virginia Rail *(Rallus limicola)* did not appear to be affected by *P. australis* (Gagnon Lupien et al., 2015). However, the authors did describe some subtle community changes: Marsh Wren appeared to prefer cattail over *P. australis* (possibly due to greater water depths in cattail habitat), while Yellow Warbler was more abundant in *P. australis* (Gagnon Lupien et al., 2015). The reason for these conflicting observations is uncertain, though analysis of bird communities rather than simply richness and abundance would likely yield greater insight. Current hypotheses for why some studies find more substantial changes in bird use following invasion than others, even within the same region, suggest that the response of the bird community to *P. australis* invasion may depend on the number or expanse of *P. australis* patches within marshes, the characteristics of *P. australis* patches, wetland water levels, and the life history of the birds being considered (Benoit and Askins, 1999; Chin et al., 2014; Gagnon Lupien et al., 2015; Whyte et al., 2015).

1.9.2 Effects on avian food sources

1.9.2-a Invertebrates

Birds are not the only wetland biota potentially affected by *P. australis* invasion. The changes caused by *P. australis* invasion are potentially capable of altering important invertebrate food sources, which could in turn affect food availability for birds. Fewer than 10 insect species are known to feed on *P. australis* in North America but the density of insects in *P. australis* stands

can be high, with sensitivity varying by macroinvertebrate taxon (Chambers et al., 1999). Snails, amphipods, and isopods are common to abundant in *P. australis* habitat, exhibiting comparable abundances with resident marsh vegetation (Fell et al., 1998). This could be because *P. australis* provides better habitat for grazing invertebrates than cattail habitat: *P. australis* patches have exhibited high diatom density, and related high densities of snails (Holomuzki and Klarer, 2010). Overall macroinvertebrate densities were observed to be similar among *P. australis, Typha* spp. and native vegetation in a Lake Erie coastal marsh (Holomuzki and Klarer, 2010). Observations from saline environments also suggested that invertebrate density and diversity is insensitive to *P. australis* invasion (Able and Hagan, 2000; Warren et al., 2001), though in one study of tidal marshes *Spartina alterniflora* supported higher macroinvertebrate abundances and species richness than *P. australis* (Angradi et al., 2001). *Phragmites australis* habitat appears to support an adequate abundance of invertebrates within marsh systems, suggesting that any observed effects on waterbirds is not simply a product of changes to the quantity of their invertebrate food.

1.9.2-b Fish

Fish comprise a significant portion of the diet of many waterbirds, such as herons, egrets, Least Bittern, and American Bittern (*Botaurus lentiginosus)*. Since *Phragmites australis* can fill-in open-water pools and reduce the depth of standing water (see below) within marshes, invasion has the potential to affect fish as a food source for these birds. However, studies comparing species composition and abundance of fish among *P. australis, Typha angustifolia,* and treated *P. australis* vegetation found no significant differences between vegetation types (Fell et al., 2003). Many studies on fish use in *P. australis* have occurred in tidal marshes, and focused on *Fundulus heteroclitus* (mummichog), a small saline tolerant killifish. *Fundulus heteroclitus* is

abundant in *P. australis,* where fish are able to successfully forage, and there are no noticeable

differences between the size of adult *F. heteroclitus* using *P. australis* and those using other

vegetation (Chambers et al., 1999; Fell et al., 2003). These fish can also successfully lay and

hatch eggs in *P. australis,* though low juvenile abundance suggests *P. australis* may not be

suitable nursery habitat (Able and Hagan, 2003). However, earlier work with fish communities

found that *P. australis* does not appear to have a negative effect on juvenile fish, including *F.

heteroclitus*, or on larger fish (Able and Hagan, 2000). In freshwater lakes in Germany, fish may

use *P. australis* stands during the day as the tall stems provide shelter from foraging birds (Okun

and Mehner, 2005). Overall the differences in the use of *P. australis* by fish appears to be

minimal, though few studies have focused on freshwater fish communities. While the interaction

between *P. australis* and fish abundance is not entirely clear, it does appear that *P. australis* can

support an adequate number of fish and, as with invertebrates, a change in use of the marsh by

birds is unlikely to be mediated solely by fish availability.

1.9.3 Effects on vegetation communities

As noted previously, *P. australis* is able to colonize wetlands quickly and produce large patches,

which can displace resident wetland plants (Ailstock et al., 2001; Trebitz and Taylor, 2007;

Tulbure and Johnston, 2010; Whyte et al., 2008). The wide range of disturbances and

environmental variables that *P. australis* can tolerate, coupled with its morphological

characteristics, contribute to *P. australis* having a competitive advantage over many resident

wetland plant species. In brackish tidal marshes *P. australis* spreads rapidly until it reaches an

equilibrium point that consists of 50-80% occupation of the marsh surface (Lathrop et al., 2003).

With this level of occupation, *P. australis* invasion has a noticeable effect on the vegetation

community in wetlands and has been noted to significantly reduce floristic diversity (Chambers et al., 1999; Keller, 2000). Decreases in plant species richness following invasion are most pronounced in freshwater marshes (Meyerson et al., 2000), where reductions in species richness are correlated to the density of *P. australis* stems (Lenssen et al., 2000; Price et al., 2014), suggesting an effect of competition between *P. australis* and native plant species. Some attribute this to the production of allelopathic gallic acid by invasive *P. australis* (Rudrappa et al., 2007; Uddin et al., 2014), thought this remains controversial (Weidenhamer et al., 2013). Given the rapid shoot production, long growing season, and great height and density of most *P. australis*; it is capable of decreasing available sunlight for native plants (Hirtreiter and Potts, 2012).

Above-ground, *P. australis* can reach 4 meters in height and patches have shoot densities ranging from 13 – 125 stems per m^2 (Meyerson et al., 2000). In Long Point, counts of living stems reached over 70 stems per m^2, and living and dead stems combined reached over 190 stems per m^2 (Rooney unpublished data). The height and density of *P. australis* allows it to dominate canopies (Minchinton and Bertness, 2003). In a comparison of light profiles between *Typha* spp. and *P. australis* patches in Long Point on average 31% of incident light reached the litter layer in *Typha* spp. compared to 17% in *P. australis* (Robichaud unpublished data). Similar results were found in Lake Erie coastal marshes in New York, and suggests that the availability of light in *Typha* stands can be exploited by *P. australis* (Hirtreiter and Potts, 2012). For other species, shading can restrict the growth of shorter plants in *P. australis* patches, especially after mid-summer when day lengths shorten and light availability decreases (Haslam, 1971b). While the above-ground biomass of *P. australis* can alter light availability to other marsh plants, the rhizomes and roots of *P. australis* also contribute to its invasive potential. *Phragmites australis* can alter below-ground competitive interactions by producing extensive root and rhizome

networks which reach up to 1 m in depth, and are typically deeper than resident plants (Moore et al., 2012). This consistently deeper root profile may circumvent nutrient competition for *P. australis,* and create niche differentiation among *P. australis* and resident wetland plants (Mozdzer et al., 2016).

There is also evidence that *P. australis* invasion may indirectly reduce native plant diversity. Muskrats are an important driver of plant diversity through canopy gap creation (Warren et al. 2001). *Phragmites australis* is known to be less palatable to muskrats, and the reduction in gap dynamics through muskrat exclusion may result in fewer bare patches and decreased opportunities for other wetland species to colonize invaded marshes (Warren et al. 2001).

Regardless of the mechanisms by which *P. australis* invasion leads to reduced floristic diversity, be they direct or indirect, it is evident that invasion often leads to substantial changes in wetland plant communities (Keller, 2000; Price et al., 2014; Wilcox et al., 2003). It is possible that reduced floristic diversity, the replacement of insect pollinated plants with wind pollinated *P. australis*, and the increased stem density and canopy closure would affect the marsh habitat value for waterbirds, especially marsh-nesting species that forage and build nests in emergent vegetation.

1.9.4 Effects on ecological processes

The changes to wetland plant communities following invasion by *P. australis* are known to significantly alter important ecological processes in wetlands. The introduction of non-native *P. australis* in a wetland ecosystem increases litter accumulation (Rooth et al., 2003; Windham, 2001), and *P. australis* stands directly increase the above- and below-ground biomass in aquatic

ecosystems, with marshes exhibiting a 3 – 10-fold increase in above-ground biomass after *P. australis* colonization (Meyerson et al., 2000; Windham, 2001; Windham and Lathrop, 1999).

Not only does *P. australis* increase net primary production, but it also appears to reduce decomposition. The litter generated by tall, dense stands of *P. australis* has a direct effect on an ecosystem because it decomposes slowly: e.g., in a shallow freshwater lake *P. australis* leaves and stems took 242 and 574 days, respectively, to reach 50% breakdown (Ágoston-Szabó and Dinka, 2008; S. R. Warren et al., 2001). *Phragmites australis* also reduces decomposition rates indirectly by shading soil and reducing soil temperature (Windham and Lathrop, 1999). Litter fills in substrate holes, smoothing microtopography and raising soil elevation which alters hydrology and lowers the depth of standing water in marshes (Able et al., 2003; Weinstein and Balletro, 1999; Windham and Lathrop, 1999). The net result is invaded marshes become drier and standing water becomes shallower over time, a change that could alter the use of marshes for birds that rely on standing water or the interface between emergent vegetation and open-water pools for foraging.

Phragmites australis may cause changes in wetland ecological processes, but these changes can take decades to become evident. In coastal tidal marshes, the peak standing crop of *P. australis* was tripled in 20 year old stands relative to five year old stands (Rooth et al., 2003). Lower standing water and smooth, elevated soil surfaces stabilize when stands are 8 to 15 years old in brackish tidal marshes (Windham and Lathrop, 1999), and 20 year old *P. australis* stands have levels of litter accretion 3 – 4 mm/year higher than adjacent younger stands (Rooth et al., 2003). Thus, we might expect that the effects of *P. australis* invasion will exhibit time lags, especially any indirect effects. For examples, if it takes 15 years for open-water patches to infill,

any effects of invasion on waterbirds that are mediated by changes in the availability of open-water patches will not be immediately apparent.

1.9.5 Effects on hydrology

I described above mechanisms by which *P. australis* invasion can decrease the extent of standing water (Weinstein and Balletro, 1999; Windham and Lathrop, 1999), reducing the extent of open-water ponds and increasing the homogeneity of the marsh habitat. The roots of *P. australis* are dense and have very resilient rhizomes that stabilize soil and enhance gas diffusion into the rhizosphere (Bart and Hartman, 2003; Moore et al., 2012), and as described above, invasion tends to dry soils and infill open-water patches (Rooth et al., 2003; Windham and Lathrop, 1999). Within dense stands the accumulation of above-ground litter and below-ground material, driven by rhizomes mats, fills in creeks and standing water pools to the point where increases in marsh elevation make flooding rare (Able et al., 2003).

Phragmites australis can also alter run-off processes in invaded marshes. Raichel et al. (2003) observed that the smooth topography created by *P. australis* infilling encourages sheet flow which can cause faster water flow than typical rivulet hydrology (Raichel et al., 2003). In contrast, Weinstein and Balletro (1999) describe how the high stem density and litter density in *P. australis* can actually reduce run-off in invaded marshes.

These hydrologic changes combine to increase the aeration of wetland soils, which can reduce the anoxia stress experienced by wetland plant roots (Moore et al., 2012), potentially altering competition dynamics in an environment where resident plant species are adapted to inundated soils. With shallower standing water (Rooth et al., 2003), elevated and smoothed topography, and reduced flooding (Able et al., 2003) and surface run-off (Weinstein and

Balletro, 1999), portions of the marsh may more closely resemble the upland environment. In terms of waterbirds, this can reduce habitat availability for waterfowl, herons, bitterns, and other species that preferentially use deeper water habitat. Whereas birds favoring robust emergent vegetation with less sensitivity to water levels, such as sparrows, blackbirds and warblers, may gain habitat following *P. australis* invasion.

1.10 Conclusion

The marshes of Long Point comprise a significant portion of the total wetland habitat along the north shore of Lake Erie, and represent bird habitat of international importance. A number of marsh-nesting bird species rely on these marshes for breeding, including the threatened Least Bittern. However, the vital role these marshes play is threatened by an on-going invasion of *P. australis.* This introduced aquatic grass is capable of converting diverse marsh vegetation communities into *P. australis* dominated habitat in just a few years. After invading a wetland, *P. australis* has been documented to reduce standing water, fill in open-water pools, decrease floral diversity, produce high rates of litter, and create dense stands that impede faunal movement. Despite these reported ecosystem effects, research conducted over 12 years ago in Long Point during the earlier stages of invasion, found that *P. australis* provided suitable habitat for many birds. While *P. australis* supported fewer marsh-nesting species individuals, overall *P. australis* supported higher total abundance and species richness than cattail or meadow marsh.

1.11 Thesis structure

In chapter 2, I seek to characterize the effects of *P. australis* invasion on bird use within Long Point marshes after over 12 years of invasion progression. The objective of this chapter is to

compare the bird abundance, species richness, and community composition of birds using invaded habitat with those using uninvaded habitat within the marshes of Long Point by contrasting *P. australis,* cattail, meadow marsh, and open-water habitat. My work is designed to build on the work by Meyer et al. (2010), while addressing gaps in the original study design. Because of *P. australis'* ability to fill in open-water pools, I have added an assessment of open-water ponds in Long Point that are threatened by on-going *P. australis* advancement. I hypothesize that **1) marsh-nesting birds will be less diverse and less abundant within *P. australis* stands than other vegetation types**. As observed by Meyer et al. (2010) and Schummer et al. (2012) in Long Point, I anticipate that after 12 years of invasion *P. australis* stands may support fewer marsh-nesting individuals than uninvaded habitat. I hypothesize that **2) overall bird diversity in *P. australis* will be lower than other vegetation types, and bird species observed in *P. australis* will be a subset of birds seen in cattail and meadow marsh habitat.** Based on work which observed few novel or rare species utilizing *P. australis,* but rather birds that have a wide distribution within the marsh such as Red-winged Blackbirds (Benoit and Askins, 2002; Wells et al., 2008; Whyte et al., 2015), I anticipate that most of the birds using *P. australis* in Long Point will be present in other vegetation types.

I also want to examine if a beneficial edge effect still occurs between vegetation types after invasion has progressed, so I will contrast bird use based on location – whether a stand is edge habitat, within 50 m of another habitat type, or interior, greater than 50 m from another vegetation type in accordance with Meyer et al. (2010). I hypothesize that **3) that the abundance and diversity of birds will be higher in the edge stands of all three habitat types.** Some studies have found birds use these habitat boundaries frequently, even if they do not use the interior of *P. australis* patches (Benoit and Askins 1999, Meyers et al. 2010, Schummer et al.

2012). In addition to bird abundance and richness, I want to examine the effects that *P. australis* may have on bird communities by assessing the effects on bird species composition and functional traits (e.g. diet, foraging strategy, nesting behaviour). I hypothesize that **4) *P. australis* habitat will support a community of birds that eat insects and are shrub nesters.** I expect that birds that forage using stalking or probing will find dense patches of *P. australis* difficult foraging habitat*,* and that *P. australis* stands may be drier and not support the food sources certain stalking or probing species require. Further, other studies have suggested that *P. australis* does not provide suitable habitat for ground nesting birds, as many ground nesters prefer dense grass and sedge meadow rather than the stiff stem and leaf material of *P. australis* (Meyer et al., 2010; Riffell et al., 2001).

In chapter 3, I present a synthesis of my findings, suggestions for measuring effects of invasion on bird communities, and comment on the implications and significance of this research in the context of wetland management in the face of biological invasions.
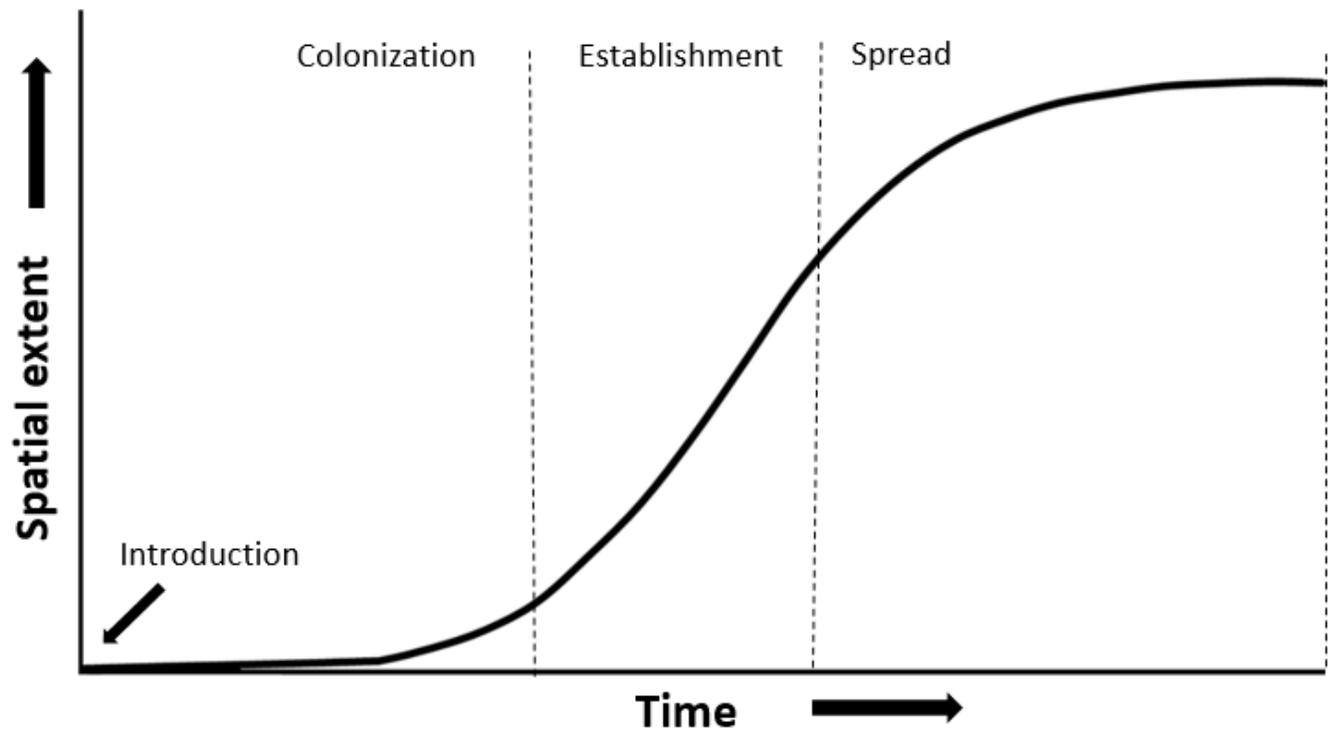
Figure 1-1. Invasion curve identifying the stages of invasion: introduction, colonization, establishment and spread. Figure adapted from Theoharides and Dukes, 2007 and Davis, 2009.

2.0 Effects of Phragmites australis *invasion on bird communities in Long Point, ON*

2.1 Introduction

The introduced clonal grass *Phragmites australis* (hereafter *P. australis*) is aggressively

colonizing freshwater coastal marshes and displacing resident vegetation communities with

dense, monotypic stands (Trebitz and Taylor 2007; Whyte et al. 2008; Tulbure and Johnston

2010). *Phragmites australis* out-competes the plant species historically characteristic of cattail

marsh and meadow marsh habitats (Wilcox et al., 2003) and fills in open-water pools (Able et

al., 2003). Not only does this reduce floristic diversity (Keller, 2000), but invasion has the

potential to threaten the highly-valued coastal-marsh habitat used by unique wetland birds,

including species at risk like Least Bittern (*Ixobrychus exilis*). Recent declines in marsh bird

occupancy, specifically Virginia Rail (*Rallus limicola)*, in Great Lakes coastal wetlands have

been attributed in part to invasion by *P. australis* (Tozer, 2016). However, research into the

effects of *P. australis* invasion on bird use sometimes suggests that the results of invasion are

benign (e.g. Meyer et al., 2010).

     As the *P. australis* invasion expands, it alters environmental conditions in the marsh. For

example, the horizontal leaf orientation of *P. australis* combines with its rapid growth and great

canopy height to lower light availability under the canopy (Hirtreiter and Potts, 2012;

Minchinton et al., 2006). We measured light extinction in 15 plots of *Typha* spp. and 15 *P.*

australis stands in Long Point, Ontario on Lake Erie, and found that on average 31% ($\pm$ 22) of

incident light reached the litter layer in *Typha* spp., compared with 17% ($\pm$ 18) in *P. australis*

(Rooney unpublished data)*.* Stem counts find that invasive *P. australis* stands are denser than the

native lineage of *P. australis*: typically, around 28 live stems per m^2 (Holdredge and Bertness,

2011; Price et al., 2014) or around 80 stems per m^2 when considering both living and dead biomass (R. S. Warren et al., 2001). In Long Point, established *P. australis* patches had stem densities of up to 76 live stems per m^2 and over 190 stems per m^2 where live and dead stems were both counted (Rooney unpublished data). The net result is that marsh habitat invaded by *P. australis* is darker and denser. It has been argued that the density of stands and rigidity of stems can make the habitat impenetrable to large-bodied waterbirds (Benoit and Askins, 1999; Kessler et al., 2011). Further, the increased above-ground biomass couples with high litter accumulation (Rooth et al., 2003; Windham, 2001) to smooth microtopography, raise soil and reduce standing water levels (Lathrop et al., 2003; Weinstein and Balletro, 1999; Windham and Lathrop, 1999), eliminating open-water pools and creeks (Able et al., 2003). Standing water and open-water pools are essential habitat for waterbirds and shorebirds, contributing to the overall heterogeneity of marshes and correlating with an increase in bird species richness, especially in meadows (Benoit and Askins, 1999; Riffell et al., 2001). These changes in habitat quality and loss of open-water habitat could affect bird use in invaded marshes.

Indeed, multiple studies have examined the effects of *P. australis* invasion on the abundance and richness of birds (Benoit and Askins, 1999; Gagnon Lupien et al., 2015; Meyer et al., 2010; Schummer et al., 2012; Wells et al., 2008; Whyte et al., 2015), but with conflicting results. Some authors show substantial changes in bird abundance (Schummer et al., 2012; Whyte et al., 2015) whereas others find little effect on bird use (Gagnon Lupien et al., 2015). Further, species richness has been found to increase with some studies (Meyer et al., 2010), and decrease with others (Benoit and Askins, 1999), making it difficult to tease apart the effects of *P. australis* invasion on wetland birds.

Over a decade ago, emerging concerns about *P. australis* invasion in Long Point, Ontario prompted a study by Meyer et al. (2010) examining the effects of invasion on bird abundance and species richness. Though present in Long Point since before 1945, the population of invasive *P. australis* began to grow exponentially in Long Point in the late 1990s (Wilcox et al. 2003). Long Point is a sandspit extending into Lake Erie from the Canadian shore. Its inner margin supports valuable coastal marsh that comprises more than 70% of the wetland habitat on the north shore of Lake Erie (Ball et al., 2003) and it provides essential habitat for numerous marsh-nesting bird species. Its position and size make it a critical stopover for hundreds of migrating bird species using the Atlantic flyway (Bird Studies Canada, 2016). It has been consequently designated as a Ramsar wetland, a UNESCO World Biosphere Reserve, and an Important Bird Area.

Based on surveys conducted in 2001 and 2002, Meyer et al. (2010) found that the total abundance and species richness of birds were higher in *P. australis* than in uninvaded cattail and meadow marsh habitats. In addition, the authors reported a strong, positive edge-effect, whereby the total abundance and species richness of birds was highest in *P. australis* stands that were within 50 m of a different vegetation type. Although they noted that more marsh-nesting birds used meadow marsh, overall *P. australis* appeared to provide suitable habitat for many birds (Meyer et al., 2010). More recently, Gagnon Lupien et al. (2015) also reported minimal effects of *P. australis* invasion on the bird communities in marshes in southwestern Quebec. In contrast, research from Virginia (Paxton, 2006), New York (Wells et al., 2008) and Connecticut (Benoit and Askins 1999) report that generalist bird species like Red-winged Blackbird (*Agelaius phoeniceus*) increase in abundance following *P. australis* invasion at the expense of wetland

specialists like Virginia Rail and Least Bittern. These authors conclude that *P. australis* invasion reduces the value of marsh habitat to birds.

One possible explanation offered for the discrepancy is that the effect of *P. australis* invasion on birds may exhibit a time lag, and changes to the bird community may become more evident as the invasion progresses (Gagnon Lupien et al., 2015). During the decade since the Meyer et al. (2010) study, *P. australis* has spread in Long Point unchecked, allowing stands to increase in size and density. Research from McMaster University indicates that *P. australis* is still rapidly expanding in Long Point (Marcaccio and Chow-Fraser, 2016). I sought to determine whether the bird community is now experiencing more notable changes, and thus repeated the assessment by Meyer et al. (2010) thirteen years after their field work was conducted.

The purpose of my study was to understand the effect that long-term, uncontrolled invasion has on bird abundance and diversity, both in terms of total birds and marsh-nesting species. Studies reporting more substantial effects of *P. australis* invasion on bird use typically observed a shift in community composition, rather than a decrease in total abundance or diversity (but see Wells et al. 2008). Thus, I also tested for changes in community composition, particularly those that alter the balance of bird functional traits, such as nesting preferences, diet, or foraging behaviour. Such changes would have ramifications for coastal marsh ecological processes and function. Further, I added bird surveys in open-water habitat to the experimental design employed by Meyer et al. (2010), since the loss of open-water associated with *P. australis* invasion could have important consequences for bird communities that would go undetected if open-water habitat was not considered.

2.2 Methods

2.2.1 Field methods

Surveys took place in 2015 and spanned three management zones in Long Point, ON – Big

Creek National Wildlife Area, Crown Marsh, and Long Point Provincial Park (Fig. 2-1).

According to the Great Lakes Water Level dashboard (Gronewold et al., 2013), Lake Erie water

levels were high in 2015, peaking at 60 cm above average in July.

I did not have access to the original data from Meyer et al. (2010), but sought to replicate

the design of the study as closely as possible. In 2014, I revisited the point count locations in

Long Point Provincial Park and Crown Marsh that Meyer et al. (2010) sampled in 2001 and

2002. Of the original 36 sites I surveyed, 20 were now invaded by *P. australis* in contrast with

six reported as invaded in 2002. New sites were established to rebalance the experimental design.

Further, I incorporated open-water habitat in the form of small pools and channels occurring in

the marsh as a new vegetation type in the design.

In 2015, I surveyed 48 fixed-distance point count locations, 22 of which had been used

by Meyer et al. (2010) and 26 that were newly established (Fig. 2-1; Appendix 8). Point count

locations were established in late April and were located a minimum of 200 m apart from each

other to ensure independence in bird observations, in keeping with similar studies (e.g., Benoit,

L.K., Askins 1999; Meyer et al.2010). Twelve point counts were located within each of four

vegetation types: 1) *P. australis,* 2) cattail marsh, 3) meadow marsh, and 4) open-water

(Appendix 3). Of each set of twelve point count locations, six were situated within 50 m of

another habitat type (edge) and six were situated greater than 50 m from any other habitat type

(interior). An exception was that all twelve open-water point count locations were situated in

edge territory, as the open-water pools or channels were less than 50 m across and incorporated

both open-water and emergent vegetation within the point count diameter. Since no patch of open-water was large enough to be greater than 50 m from another habitat type on all sides, it was impossible to separate these sites into "interior" open-water and "edge" open-water.

I surveyed vegetation at each point count location in mid-August to facilitate bird habitat characterization. Three 1 m^2 quadrats were established 10 m from the center of the point count location and the average canopy height, percent cover of plant species, and water depth were recorded to characterize the habitat present at each point count location. In general, meadow marsh point count locations were characterized by shallow standing water or saturated soils, and dominated by hummock forming grasses (*Calamagrostis canadensis)* and sedges (*Carex* spp.) (Appendix 3-C). Cattail marsh point count locations were inundated throughout the growing season and dominated by *Typha* spp. (Appendix 3-B), while *P. australis* point count locations spanned a moisture gradient between cattail marsh and meadow marsh soil-saturation levels and were dominated by the invasive *P. australis* haplotype (Appendix 3-A). Open-water point count locations were pools or slow moving channels within the marsh complex characterized by lilies (*Nuphar lutea* and *Nymphaea odorata*), *Potamogeton* spp., and *Chara* spp. (Appendix 3-D, Appendix 4).

I surveyed birds at each point count four times throughout the summer (May to early August 2015), separated by a minimum of 10 days. Surveys followed the protocol adopted by Meyer et al. (2010) and the recommendations of Bird Studies Canada (2009). In brief, between half an hour after sunrise and 09:30, point count surveys took place from an established center point on a 1.8 m ladder to standardize observer height and vantage point, as canopy height differs by vegetation type (Table 2-1). All individual birds seen or heard within a 25 m radius around the center point, or actively foraging within 100 m above were identified and recorded. Birds that

flew over or through the survey site without using it were noted but not used in data analysis. Surveys were 15 minutes in length and consisted of 5 minutes of passive listening, 5 minutes of call broadcasting for secretive birds, including Virginia Rail, Sora (*Porzana carolina*), Least Bittern, a combination of Common Moorhen (*Gallinula chloropus*) and American Coot (*Fulica americana*), and Pied-billed Grebe (*Podilymbus podiceps*), and a final 5 minutes of passive listening.

2.2.2 Statistical methods

Birds were classified as marsh-nesters if they nest in wetlands, or generalists if they do not require wetlands for nesting, in keeping with the classification by Meyer et al. (2010) (Appendix 5). Marsh-nesting species in decline in the lower Great Lakes (Tozer, 2016) were further classified as marsh-nesting species of concern (Appendix 5). Analyses were performed on six response variables: total bird abundance, total species richness, marsh-nesting bird abundance, marsh-nesting species richness, bird community composition, and functional trait composition. Functional traits included foraging behaviour (e.g., ground forager, stalking, aerial forager), diet (e.g., insects, seeds, fish) and nesting preferences (e.g., cavity, shrub, ground), in agreement with traits reported in the Birds of North America Online resource (Rodewald, 2015). Bird counts were summed across all survey dates to capture birds that call or use the marsh at different times in the summer (Appendix 6).

2.2.2-b Abundance and species richness

First, the total abundance of birds of each species was summed for each point count to generate the total bird abundance values. Second, to calculate the abundance of marsh-nesting birds, only the abundance of species identified as marsh-nesters in Appendix 5 were summed. Third, the total number of species observed at each point count throughout the summer was summed to represent bird species richness. Finally, the total number of marsh-nesting species at each point count was summed to determine marsh-nesting bird species richness. All univariate analyses were performed using R (R Core Team 2016).

To determine whether bird abundances or species richness differed among the four vegetation types (*P. australis,* cattail marsh, meadow marsh, open-water) I used a one-way ANOVA with type III sums of squares. To evaluate differences in bird abundance or species richness between edge and interior loci, I assessed only *P. australis*, cattail marsh, and meadow marsh vegetation types as all open-water sites were edge habitat. I conducted a two-way ANOVA with an interaction term, with locus and vegetation type as factors. I found that the interaction term was not significant so I used type II sums of squares in the two-way ANOVAs. For both one-way and two-way ANOVAs, a Tukey's pairwise comparison was performed when F-values were significant ($p < 0.05$).

2.2.2-c Community composition and functional traits

I performed multivariate analyses to characterize the differences in bird community composition and functional traits in different vegetation types and between loci, using PC-ORD (McCune and Mefford, 2011). Data underwent general relativization to reduce the influence of highly abundant species, such as Red-winged Blackbirds. In addition, I excluded rare species (< 2 occurrences) to reduce data sparsity prior to ordinations, as recommended by Peck (2010).

To visualize differences in community composition and functional traits, I calculated Bray-Curtis dissimilarity matrices (Bray and Curtis, 1957) for both species counts and counts of different functional traits, and performed non-metric multidimensional scaling ordination (NMS) on each matrix separately. Each point in the NMS figures represents a point count location, and they are positioned such that proximity in the figure is correlated with similarity in either community composition or functional traits, depending on which matrix was used in the NMS. The best ordination solutions were determined using an iterative process with a random starting configuration, comparing solutions with one to four dimensions, using 50 runs with real data and 50 runs with random data. The best fitting ordination solution for each matrix was re-run to quantify the stress and instability of the final solution. Two meadow marsh sites had undue influence on axis 1 for both species abundance and functional traits, so I re-ran the ordination excluding these sites. Their removal did not alter the interpretation of the ordinations, so I present the ordinations excluding these two sites.

Since open-water habitat did not permit interior point count locations, analyses including the open-water vegetation type could not consider the factor locus. Hence, a multi-response permutation procedure (MRPP) with a Bray-Curtis distance measure (Zimmerman et al., 1985) was used to assess the significance of differences among bird assemblages in open-water, meadow marsh, cattail marsh, and *P. australis* vegetation types.

MRPP permits an unbalanced design; however, where a balanced two-factor experimental design is possible (i.e., where only meadow marsh, cattail marsh, and *P. australis* vegetation types were contrasted) permutational MANOVA (perMANOVA) is preferable because it allows the analysis of a two-factor design with an interaction term (Anderson and Walsh, 2013; McCune and Grace, 2002). Thus, for the *P. australis*, meadow marsh and cattail

marsh vegetation types, which possessed both interior and edge habitats, the significance of observed differences in community composition among vegetation type, locus, and their interaction (i.e., whether the influence of vegetation type on community composition differed between loci) were tested using perMANOVA where there were equal numbers of point counts per treatment (Anderson, 2001).

2.2.2-d Vegetation analyses

The relative cover of the dominant plant species within each vegetation type was calculated based on the total vegetation cover, excluding bare soil and litter. Simpson's reciprocal diversity index was calculated as described in Hill (1973) as

$$1/\sum(n/N)^2$$

2.3 Results

I observed 32 bird species, including 12 marsh-nesting species (Appendix 4), during the 2015 field season. In total, 22 species were found in open-water, 21 in meadow marsh, 17 in cattail marsh, and 13 in *P. australis* (Appendix 6). In comparison, Meyer et al. (2010) found 28 bird species in meadow marsh, 18 in cattail marsh, and 27 in *P. australis* during the breeding season. The four vegetation types differed in terms of habitat structure as well as dominant vegetation species (Table 2-1, Appendix 4).

2.3.1 Abundance and species richness

The interaction terms for total abundance and species richness were never significant (p > 0.05), nor was locus (p > 0.05); however, I observed significant differences in abundance among vegetation types (Table 2-2; Fig. 2-2B). For marsh-nesting bird abundance and species richness the interaction term was never significant (p > 0.05), nor was locus (p > 0.05), nor vegetation type (p > 0.05). However significant differences in marsh-nesting bird abundance were observed when open-water was considered (Table 2-2; Fig. 2-3B), as open-water habitat supported the fewest individuals but an equivalent number of species as other vegetation types. *Phragmites australis* patches support fewer individuals than meadow marsh, and significantly fewer individuals than cattail marsh habitat.

The abundance of marsh-nesting birds was significantly (p = 0.002) influenced by vegetation type when open-water was considered, and driven by the difference between open-water and cattail marsh. The number of individual marsh nesters and marsh-nesting species were comparable between cattail marsh, meadow marsh, and *P. australis* (Figure 2-3).

2.3.2 Community composition and functional traits

The optimal NMS ordination of the community composition dissimilarity matrix had two dimensions, with an acceptable final stress (18.54) and a final instability of <0.001 after 61 iterations. This ordination solution explained 77% of the variance in community composition; 52% on axis 1 and 25% on axis 2 (Fig. 2-4). Note that I tested the sensitivity of the general conclusions to the inclusion of open-water point count locations in the NMS by repeating the ordination without the open-water data and found the general interpretation unchanged (Appendix 7).

A strong moisture gradient is correlated with the differences in community composition summarized by Axis 1, separating deeper open-water sites from the shallower point count locations. Meadow marsh is the shallowest of the four vegetation types, while *P. australis* grows in a range of water depths (Table 1). Consequently, there is overlap in bird community composition between *P. australis* point count locations and those in cattail marsh and meadow marsh on Axis 1. Axis 1 reflects a trend in the abundance of smaller-bodied marsh-nesting species Common Yellowthroat (*Geothlypis trichas)* and Swamp Sparrow (*Melospiza georgiana*), which are associated with shallower areas with more vegetation ground cover. Due to the differences in species composition and lower abundance of birds using the open-water pools and channels, open-water point count locations also group separately on Axis 1. Open-water sites support waterfowl not found in any other vegetation type. There is some overlap between cattail marsh and open-water point count locations, as open-water locations included emergent vegetation and cattail marsh also provides areas of deeper water that support species such as Marsh Wren. Axis 2 in the ordination is driven by trade-offs between Canada Goose (*Branta canadensis*) and Wood Duck *(Aix sponsa)*, and swallows (*Hirundinidae*), with the aerial foraging swallows associating with open-water and meadow marsh point count locations (Fig. 2-4). Other aerial insectivores that hunt via fly-catching, Willow Flycatcher *(Empidonax traillii)* and Eastern Kingbird *(Tyrannus tyrannus)*, used *P. australis* in addition to meadow marsh and cattail marsh. Canada Goose and Wood Duck are strongly associated with open-water habitat, rarely using any other vegetation type. Swamp Sparrow, in contrast, was more abundant in meadow marsh, and rarely used open-water locations. Swamp Sparrow is also more associated with meadow marsh than Common Yellowthroat, though both species occurred more often in meadow and cattail marsh than in *P. australis.*

In visualizing patterns in bird functional traits, the optimal NMS solution had three dimensions with low final stress (9.59) and a final instability of <0.001 after 90 iterations. The ordination solution explained a cumulative 92% of the variance; 68% axis 1, 15% axis 2, and 8% axis 3 (Fig. 2-5). As in the ordination on species composition, Axis 1 was strongly correlated with a water depth: deeper open-water point count locations separated from cattail marsh, *P. australis*, and meadow marsh. Axis 2 reflects differences in diet and foraging behaviours, with *P. australis* sites clustering closely together. Birds that consume plants, fish, or seeds and utilize stalking or dabbling foraging techniques were associated with open-water or deeper cattail marsh. Birds that forage on the ground (gathering food from shallow water or low branches) or glean from foliage and mainly consume insects are found in shallower vegetation types. The third axis is driven by aerial foragers associating with open-water and meadow marsh, and ground nesting species associating with open-water habitat. Insectivorous, shrub nesting, foliage gleaning or ground foraging species are associated with drier vegetation types, and are not found using open-water or deeper cattail marsh sites as frequently. On axis 2 meadow and cattail marsh sites are more spread out, while *P. australis* sites remain clustered on both axes.

For both community composition and functional traits, I observed no significant interaction between locus and vegetation type (perMANOVA on community composition: p > 0.05; perMANOVA on functional traits: p > 0.05), or locus (perMANOVA on community composition: p > 0.05, perMANOVA on functional traits: p > 0.05). Both the perMANOVA (contrasting *P. australis*, cattail and meadow marsh) and MRPP (contrast all four vegetation types) found that vegetation type was a significant predictor of bird community composition and functional traits (Tables 2-3, 2-4). Pair-wise comparisons of vegetation types reveal that the bird

communities associated with each vegetation type are distinct, but the bird communities in meadow and cattail marsh possess similar functional traits.

2.4 Discussion

Long Point, Canada is highly acclaimed as a biodiversity hotspot, bird stop-over and breeding site, but this Ramsar wetland, UNESCO World Biosphere Reserve, and Important Bird Area is threatened by an extensive and largely unmitigated invasion of European *Phragmites australis*. Several previous studies, including research in coastal wetlands along the Ohio shore of Lake Erie (Whyte et al., 2015) and in freshwater marshes in southwestern Quebec (Gagnon Lupien et al., 2015), concluded that the effects of *P. australis* on bird use in invaded wetlands were limited. In Long Point itself, a study carried out 2001 and 2002 reported an increase in bird abundance and species richness associated with *P. australis* patches compared with the historically dominant cattail and meadow marsh vegetation communities (Meyer et al., 2010). They also found that the edges of stands (within 50 m of another vegetation type) supported more bird species than interior habitats. In contrast, I found lower total abundance of birds in *P. australis* than either cattail or meadow marsh (Table 2-4). In some studies, where bird abundance increased with *P. australis* invasion, this was attributed to high numbers of Red-winged Blackbirds (Wells et al. 2008, Whyte et al. 2015). Although I observed high abundances of Red-winged Blackbirds in every vegetation type, they were less abundant in *P. australis* than either cattail or meadow marsh in 2015 (Appendix 6). Further, I did not observe the positive edge-effects reported by Meyer et al. (2010), detecting no difference in bird abundance, richness, or community composition between the interior and edges of the marsh vegetation types possessing interior points.

I suspect the reason there no longer appears to be an increase in abundance or richness of birds associated with *P. australis* or with habitat edges is that in the 13 years since the Meyer et al. (2010) bird surveys, *P. australis* cover has expanded and become denser. In the early stages of invasion when patches are relatively thin, *P. australis* may have contributed to overall habitat heterogeneity and provided structural diversity that is no longer present now that patches are over a decade old (Rooth et al., 2003). Supporting this hypothesis, Gagnon Lupien et al. (2015) attribute their finding that *P. australis* had no severe effect on bird use in southwestern Quebec marshes to the early stage of invasion in their study system. As *P. australis* expands, replacing meadow marsh and cattail marsh, it smooths and elevates substrate, filling in small holes and open-water pools through litter accumulation (Weinstein and Balletro, 1999; Windham and Lathrop, 1999), reducing floral diversity, and creating dense stands of stiff stems (Ailstock et al., 2001; Schummer et al., 2012; Windham, 2001). These changes alter marsh habitat making it less heterogeneous. Bird species like Swamp Sparrow, Virginia Rail, and American Bittern (*Botaurus lentiginosus)*, which prefer sedges and grasses, open-water pools, and more ground cover when selecting nesting sites (Riffell et al., 2001), therefore lose habitat area as the *P. australis* invasion becomes more established. I suspect that the loss of edge effects in Long Point is also due to the maturation of *P. australis* in the last decade. The continued growth and infilling of *P. australis* patches over time shortens the length of the ecotone between vegetation patches from a gradual gradient to an abrupt border.

In assessing the effects of invasion on any biological community, it is important to consider not only species richness, but also community composition. Species richness can be useful in describing marsh biodiversity, but it may obscure the impact of a biological invasion. This study is not alone in finding little difference in bird richness between invaded and resident

vegetation types (Gagnon Lupien et al., 2015; Whyte et al., 2015). A decline in the abundance of a species, without it being extirpated, or a switch from a sensitive specialist species to a more generalist one will not register in the measure of species richness, making it an insensitive metric. The bird community composition within a wetland is more sensitive to ecological changes than bird species richness, and should therefore be considered in determining the effects of *P. australis* invasion.

I found that bird community composition was influenced by *P. australis*, leading to further changes in bird community functional traits, i.e. the roles birds perform within the ecosystem. Bird communities using open-water, cattail marsh, meadow marsh, and *P. australis* stands are each distinct. However, the bird community in *P. australis* is not supporting novel species, but rather a novel community made up of borrowed parts. Within *P. australis,* the most abundant species observed were Common Yellowthroat, Swamp Sparrow, Marsh Wren (*Cistothorus palustris*), Red-winged Blackbird, and Yellow Warbler (*Setophaga petechia*). Excluding Yellow Warbler, all of these species were more abundant within cattail marsh or meadow marsh than in *P. australis*. The mixing of bird communities in *P. australis* could be attributed to its wide range of tolerance of soil moisture level (Engloner and Papp, 2006; Vretare et al., 2001) such that *P. australis* grows in areas formerly occupied by drier meadow marsh and by inundated cattail marsh. In Long Point in 2001-2002 (Meyer et al. 2010) and in southwestern Quebec (Gagnon Lupien et al., 2015) *P. australis* supported high numbers of Yellow Warbler, likely because this species nests in shrubs and trees, which can be mimicked by the stiff stems and density of *P. australis* stands (Gagnon Lupien et al., 2015; Lowther et al., 1999). *Phragmites australis* habitat can also provide an adequate abundance of insects to support Yellow Warbler's

diet, and the physical structure of *P. australis* allows foliage gleaners access to this food supply (Holomuzki and Klarer, 2010; Lowther et al., 1999).

Vegetation type did not yield a strong influence on marsh-nesting bird abundance or species richness, but when considering community composition and functional traits it is evident that the type of marsh-nesting species found in cattail marsh, meadow marsh, and open-water vegetation differed from those found in *P. australis*. The only marsh-nesting birds observed in *P. australis* (Common Yellowthroat, Swamp Sparrow, and Marsh Wren) were all small-bodied, shrub-nesting birds that primarily glean insects from plants (Guzy and Ritchison, 1999; Kroodsma and Verner, 2014; Mowbray, 1997). Foliage gleaning may be easier than other foraging strategies in *P. australis*, where the density of *P. australis* stems can make it difficult to maneuver, especially for larger-bodied birds (Benoit and Askins, 1999). Species such as Great Blue Heron (*Ardea herodias*), Sora, American Bittern, Least Bittern, Sandhill Crane (*Grus canadensis*), and Virginia Rail occurred only in cattail marsh, meadow marsh or open-water vegetation types. Specifically, marsh-nesting species of concern (Virginia Rail, American Bittern, Least Bittern) were not recorded using *P. australis* during the sampling period (Appendix 6). In terms of traits, species that rely on stalking or dabbling for foraging and nest on the ground were more strongly associated with meadow marsh, cattail marsh and open-water habitat than with *P. australis*. This includes the marsh-nesting species Virginia Rail, Sora, and Least Bittern, who forage for food by probing, ground foraging and stalking, respectively, and preferentially build ground nests using cattail vegetation or sedges (Conway, 1995; Melvin and Gibbs, 2012; Poole et al., 2009). American Bittern, a species observed only in cattail marsh and open-water, is also a ground nesting bird who forages via stalking and has been reported to avoid dense, even-aged stands of vegetation when hunting (Lowther et al., 2009). Similarly, aerial

insectivores like Barn Swallows (*Hirundo rustica*) were most abundant foraging over open-water and meadow marsh. Along the southern shoreline of Lake Erie, *P. australis* did not appear to negatively affect macroinvertebrate density, which suggests *P. australis* stands can provide an adequate food supply for birds (Holomuzki and Klarer, 2010). It is possible the dense above-ground stands may limit emergence or availability of macroinvertebrates for aerial foragers. Additional work is necessary to determine why these birds are not using *P. australis* habitat.

The use of open-water habitat by birds was not examined by Meyer et al. (2010), although another study conducted in Long Point compared birds in mixed-cattail habitat (*Typha* spp. and *P. australis*) with birds in open-water ponds (Schummer et al., 2012). This study concluded that total bird abundance was higher in open-water than in mixed-cattail habitat, and there were significantly more marsh-nesting individuals and species in open-water (Schummer et al., 2012). In contrast, I found lower abundance in open-water and no difference in marsh-nesting bird species richness among vegetation types. Yet, open-water sites support a distinct bird community, including marsh-nesting species such as American Bittern and Least Bittern, and other species such as Mallard (*Anas platyrhynchos*), Wood Duck (*Aix sponsa*), Blue-winged Teal (*Anas discors*), and terns (*Laridae*). The potential for *P. australis* to reduce the size of these areas or fill them entirely (Lathrop et al., 2003; Windham and Lathrop, 1999) is a threat to this open-water bird community.

The reduction in breeding habitat available for marsh-nesting birds due to *P. australis* invasion will have serious consequences for bird conservation, especially as many marsh-nesting species have already experienced significant declines around the Great Lakes (Tozer, 2016). Further, studies predict that *P. australis* will experience considerable expansion throughout the Great Lakes as climate change, altered flood regimes, and anthropogenic disturbances provide

suitable habitat for colonization (Mazur et al., 2014; Tougas-Tellier et al., 2015). Understanding the implications of invasion on important biological communities is essential to management, as *P. australis* has the potential for regional or bi-national impacts.

In Long Point, as *P. australis* continues to replace scarce meadow and cattail marsh habitat, there may not be a reduction in species richness; however, the identity and functional traits of birds present in the marsh will shift to a mix of smaller-bodied, shrub-nesting generalists like Yellow Warbler and Common Yellowthroat. These results suggest that ground-nesting birds that forage by stalking or dabbling will be most affected, including the threatened Least Bittern. The impacts of *P. australis* invasion appear to have a lag time, as what seemed to be benign or even beneficial in the early stages of invasion now clearly has negative effects on bird use in Long Point. Destruction and fragmentation of the habitat that specialized birds require for reproduction may lead to time-delayed extinction (Kuussaari et al., 2009; Tilman et al., 1994), highlighting the need to preserve large areas of cattail marsh and meadow marsh within invaded coastal marsh habitats.

My work emphasizes the importance of considering the identity and functional traits of birds to fully comprehend the effects of an invasive plant. *Phragmites australis* can exclude sensitive species that have specific habitat requirements, replacing them with generalist species and causing a shift in bird community and the functional traits of birds. Species richness is an insensitive metric for determining the effects of biological invasion on an ecosystem because such shifts are not necessarily evident unless the identity and traits of affected communities are considered explicitly. Future monitoring efforts should incorporate a measurement of species composition, rather than focusing on abundance or species richness, to capture the subtler effects of biological invasion.

2.5 Figures and Tables
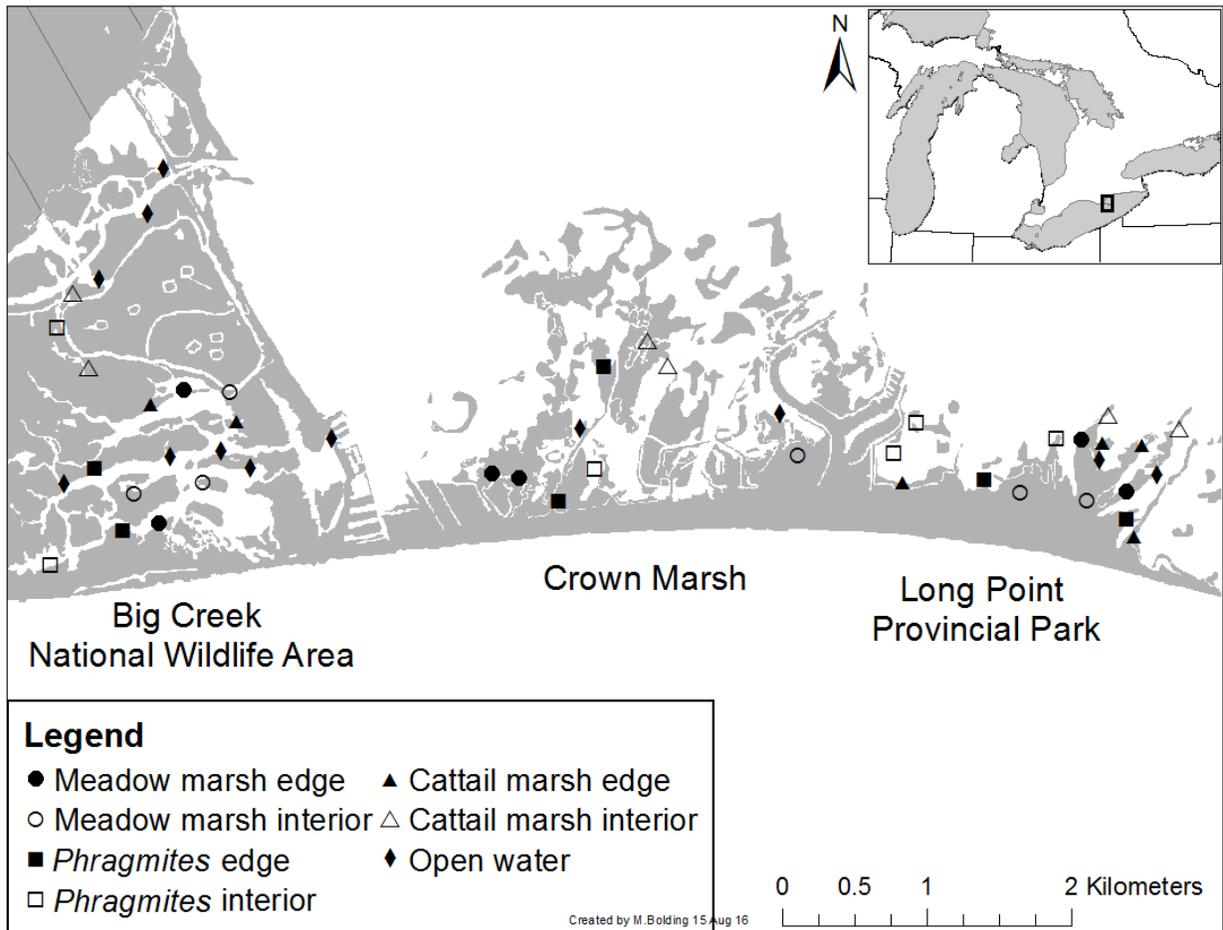
Figure 2-1 Bird survey point count locations within three management zones - Big Creek

National Wildlife Area, Crown Marsh, and Long Point Provincial Park - in Long Point, ON
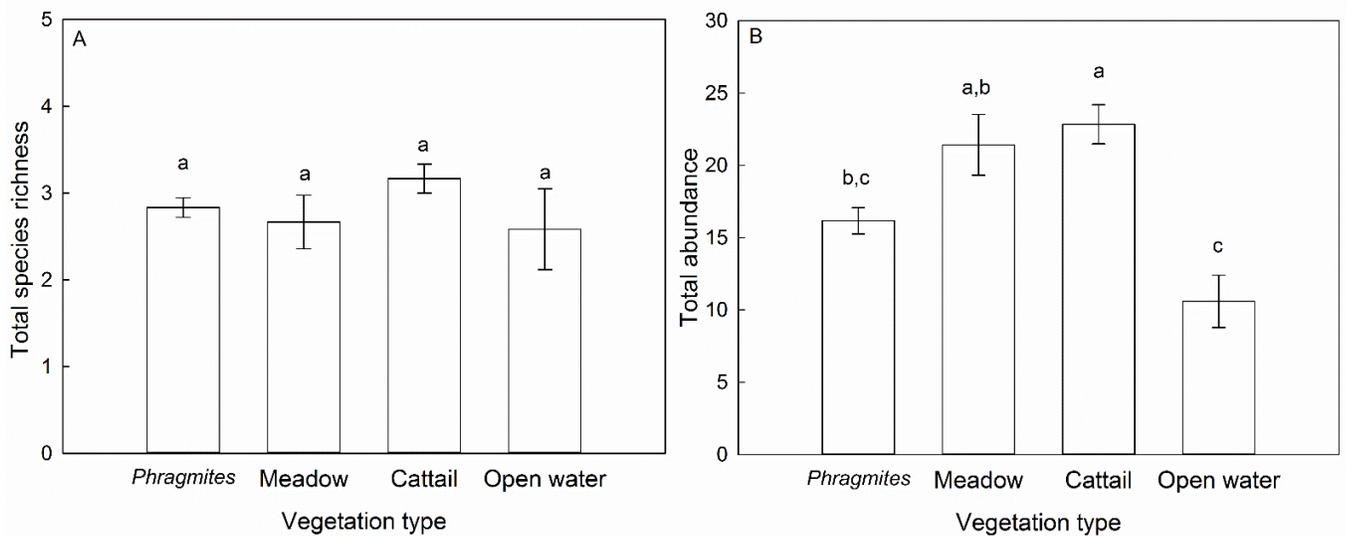
Figure 2-2. *The four vegetation types exhibited no difference in total species richness (p = 0.272) (A), but total bird abundance was affected by vegetation type (p < 0.01) (B). Total abundance based on summed occurrences and total species richness based on summed number of species at 48 point count locations in Long Point, ON. Error bars represent standard error*, lower case letters represent Tukey's HSD post-hoc comparison results. Bars with the same letter do not differ significantly.
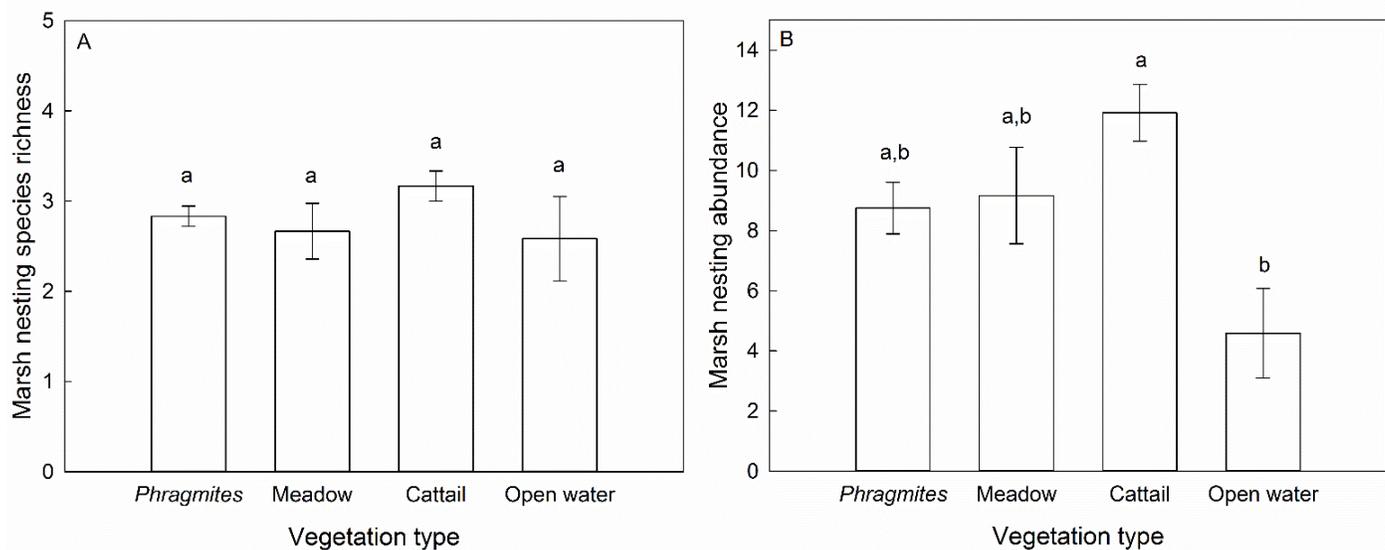
Figure 2-3. No difference in marsh-nesting bird richness among the four vegetation types (p = 0.529) (A), while abundance is affected by vegetation type (p = 0.002) (B). Marsh-nesting abundance based on summed marsh-nester occurrences and species richness based on summed number of marsh-nesting species at 48 point count locations in Long Point, ON. Error bars represent standard error, lower-case letters represent Tukey's HSD post-hoc comparison results. Bars with the same letter do not differ significantly
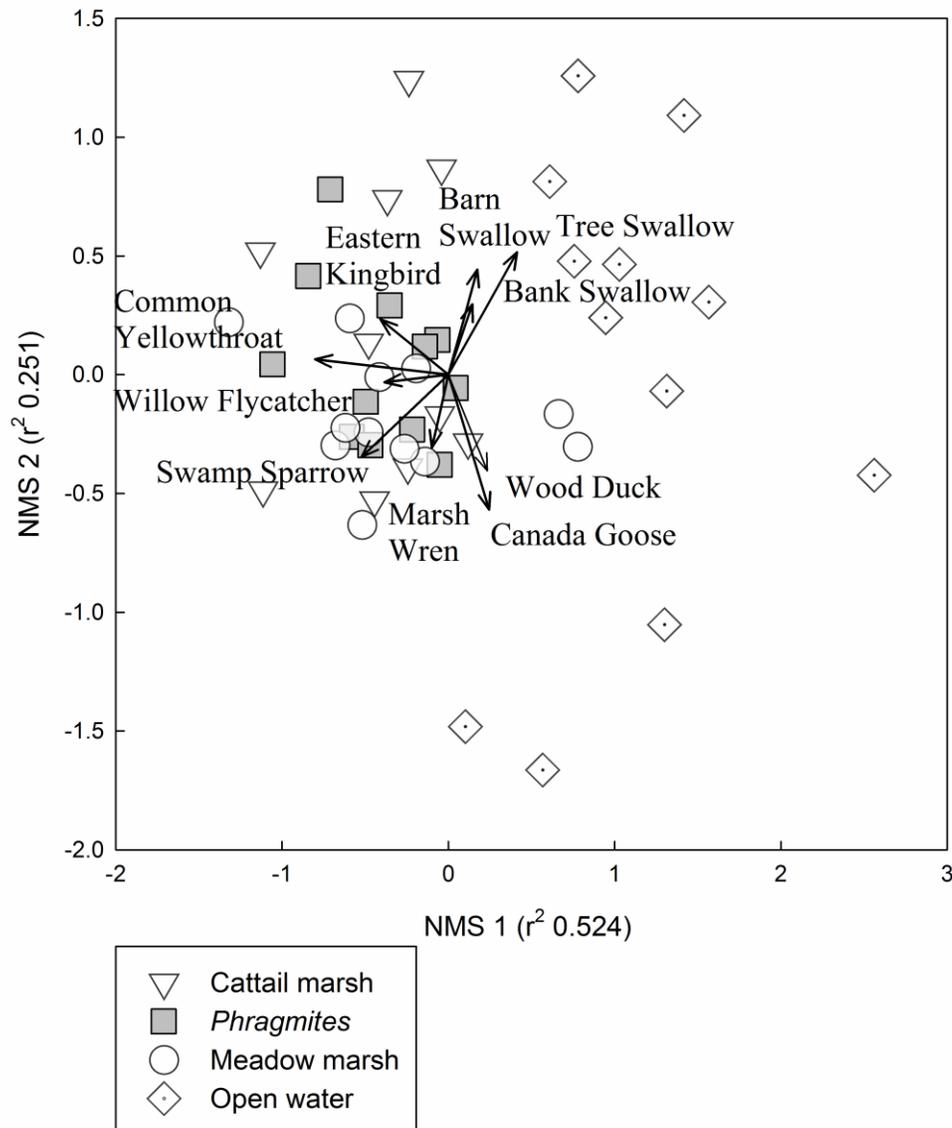
Figure 2-4. 2D NMS ordination solution of Bray-Curtis dissimilarity matrix calculated using bird species abundances with bird species vectors overlaid (final stress 18.54). In this joint plot, only species whose abundance was reasonably correlated with at least one ordination axis are depicted as vectors. Symbology of points represents the four habitat types considered: *Phragmites australis,* cattail marsh, meadow marsh, and open-water
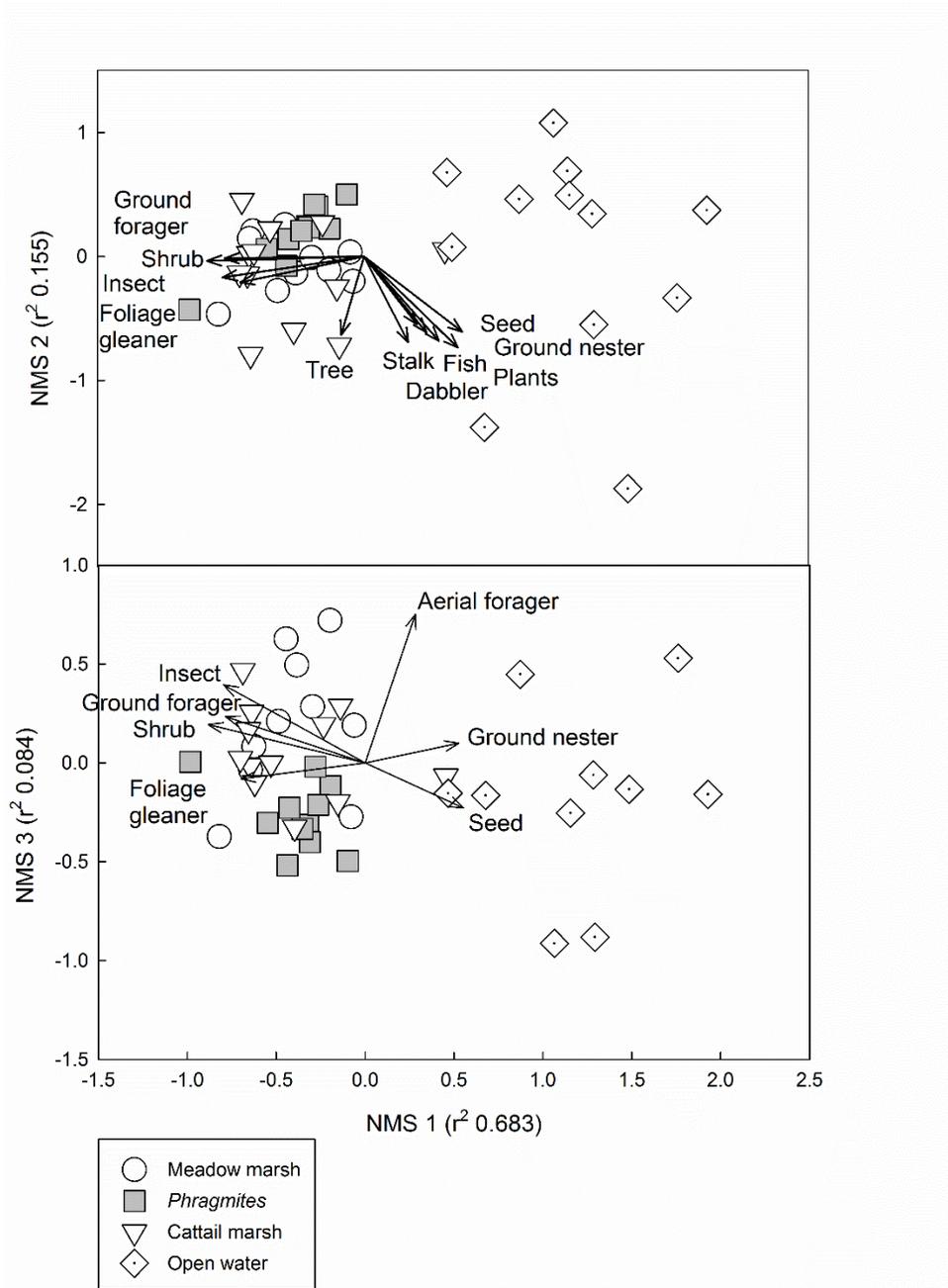
Figure 2-5: 3D NMS ordination solution of Bray-Curtis dissimilarity matrix calculated using bird species abundances with bird functional trait vectors overlaid (stress 9.59). Joint plots depict site ordination scores overlaid with bird functional traits correlated with each site. Symbology of points represents the four habitat types considered: *Phragmites australis,* cattail marsh, meadow marsh, and open-water.

Table 2-1. Vegetation and environmental characterization of the four studied vegetation types in Long Point, ON, based on twelve point count locations in each vegetation type. Simpson's diversity index calculated as $1/\sum(n/N)^2$

Vegetation Type	Dominant species (relative cover %)	Simpson's Diversity Index	Average water depth (cm) ± SD	Average canopy height (cm) ± SD
Meadow marsh	*Calamagrostis canadensis* (49.18)	3.176	19 cm ± 12 cm	93 cm ± 16 cm
Cattail marsh	*Typha* spp. (77.02)	1.768	32 cm ± 7 cm	247 cm ± 35 cm
Open-water marsh	*Nymphaea odorata* (24.16)	1.464	> 1 m	n/a
P. australis	*Phragmites australis* (72.00)	1.756	27 cm ± 14 cm	302 cm ± 35 cm

Table 2-2. Total bird abundance and marsh-nesting bird abundance were influenced by vegetation type, whereas total and marsh-nesting species richness was not influenced by any of the factors. Two-factor ANOVA results compared bird abundance and richness among three vegetation types (*Phragmites australis,* cattail marsh, meadow marsh); one-way ANOVA results compared bird abundance and richness between four (*P. australis,* cattail marsh, meadow marsh, open-water)

Response	Two-factor ANOVA			One-factor ANOVA (with open-water)		
	F	Degrees freedom	*p*	*F*	Degrees freedom	*p*
Total Abundance	4.94	2, 30	0.014	12.05	3, 44	$6.94e^{-6}$
Total Species Richness	1.74	2, 30	0.192	1.35	3, 44	0.272
Marsh-nesting Abundance	0.66	2, 30	0.523	5.73	3, 44	0.002
Marsh-nesting Species Richness	0.87	2, 30	0.431	0.75	3, 44	0.529

Table 2-3. perMANOVA contrasting species composition and functional traits among the three vegetation types possessing edge and interior point count locations *(Phragmites australis*, cattail marsh, meadow marsh). Each of the three vegetation types supported distinct bird communities. Bird functional traits in *P. australis* were significantly different from those in cattail and meadow marsh; however, functional traits in cattail and meadow marsh were similar.

perMANOVA	Species composition		Functional traits	
Vegetation types	$F_{2,35} = 2.69, p < 0.001$		$F_{2,35} = 3.15, p < 0.001$	
Post-hoc comparison	T	p	T	p
Cattail marsh x *P. australis*	1.64	0.006	1.97	0.002
Cattail marsh x meadow marsh	1.50	0.022	1.25	0.133
P. australis x meadow marsh	1.81	< 0.001	2.22	< 0.001

Table 2-4. MRPP results comparing species composition and functional traits in all four vegetation types (*Phragmites australis,* cattail marsh, meadow marsh, open-water). Each vegetation type supports a distinct bird community; however, cattail and meadow marsh vegetation types support similar functional traits.

MRPP	Species composition		Functional traits	
	A	*p*	*A*	*p*
Vegetation type	0.107	<0.001	0.192	<0.001
Cattail marsh x *P. australis*	0.042	0.003	0.095	<0.001
Cattail marsh x meadow marsh	0.026	0.034	0.003	0.350
Cattail marsh x open water	0.063	<0.001	0.201	<0.001
P. australis x meadow marsh	0.054	0.001	0.085	<0.001
P. australis x open-water	0.134	<0.001	0.244	<0.001
Meadow marsh x open water	0.108	<0.001	0.129	<0.001

Table 2-5. Comparison of results into the effects of *Phragmites australis* invasion on birds in Long Point carried out during the breeding season in 2001-2002 (Meyer et al. 2010) and 2015 results. Two-way ANOVA results are presented for all 2015 vegetation type and locus, one-way ANOVA results presented for open-water vegetation type

Response variable	Factor	2015 results	2001-2002 results
Total abundance	Vegetation type (two-way ANOVA)	*P. australis* lower, significantly lower than cattail marsh (p = 0.014)	Highest in *P. australis* (p = 0.036)
	Vegetation type (one-way ANOVA)	Open-water lowest (p < 0.001)	Open-water not considered
	Locus	No significant effect (p = 0.567)	20% higher in edge (p = 0.083)
Total species richness	Vegetation type (two-way ANOVA)	No significant effect (p = 0.192)	Higher in *P. australis* (p = 0.006)
	Vegetation type (one-way ANOVA)	No significant effect (p = 0.272)	Open-water not considered
	Locus	No significant effect (p = 0.112)	20% higher in edge (p = 0.001)
Marsh-nesting abundance	Vegetation type (two-way ANOVA)	No significant effect (p = 0.523)	Highest in meadow marsh (p = 0.047)
	Vegetation type (one-way ANOVA)	Lowest in open-water (p = 0.002)	Open-water not considered
	Locus	No significant effect (p = 0.159)	Higher in edge (p = 0.015)
Marsh-nesting species richness	Vegetation type (two-way ANOVA)	No significant effect (p = 0.431)	No significant effect (p > 0.10)
	Vegetation type (one-way ANOVA)	No significant effect (p = 0.529)	Open-water not considered
	Locus	No significant effect (p = 0.387)	No significant effect (p > 0.10)

3.0 Implications

3.1 Thesis overview

Introduced *Phragmites australis* is aggressively colonizing the coastal marshes of Long Point, ON. These marshes comprise over 70% of the wetland habitat on the north shore of Lake Erie and provide habitat for a number of provincially significant birds, including at risk marsh-dependent species such as Black Tern *(Chlidonias niger)* and Least Bittern *(Ixobrychus exilis)*. Many secretive, wetland-dependent species that rely on coastal marshes are in decline throughout the southern Great Lakes (Tozer, 2016). These declines have been attributed to urban development, decreases in wetland area, and – in the case Virginia Rail *(Rallus limicola)* – to the ongoing invasion by *P. australis* (Tozer, 2016). The invasion of Long Point by introduced *P. australis* raises concerns about the effects of invasion on bird communities, as Long Point represents a significant portion of the wetlands remaining on the north shore of Lake Erie.

Phragmites australis colonization can alter wetlands and compromise habitat that is essential for wetland-dependent bird species that require marshes for breeding and nesting. The tall, dense stands that *P. australis* produces can reduce floristic diversity (Keller, 2000), fill in open-water pools (Able et al., 2003), and restrict access for certain larger-bodied bird species (Benoit and Askins, 1999; Kessler et al., 2011). Within Long Point, where *P. australis* is replacing the historically dominant cattail and meadow marsh communities (Wilcox et al., 2003), this conversion results in more structural homogeneity as *P. australis* stands become denser and fill-in canopy gaps as they age (Rooth et al., 2003).

The population of introduced *P. australis* in Long Point grew exponentially in Long Point during the late 1990s, when low water levels facilitated its spread (Wilcox et al., 2003). This rapid expansion motivated research into the effects of the *P. australis* invasion on bird

communities in 2001-2002. Comparing birds in *P. australis* with the meadow marsh and cattail marsh habitats that it was replacing, research carried out during this rapid expansion stage of the invasion found higher total abundance and species richness of birds in *P. australis* habitat, especially around its edges (Meyer et al., 2010). Marsh-nesting birds specifically had lower abundances in *P. australis* however, in general this earlier research concluded that *P. australis* invasion is benign for birds in Long Point. The goal of my thesis was to evaluate the changes in bird occupancy within Long Point's marshes after years of unmitigated *P. australis* invasion progress. My work was designed to build on the Meyer et al. (2010) study, which took place over ten years ago.

3.2 Research Conclusions

In my 1st chapter I established the context of *P. australis* invasion in wetlands, and the potential deleterious effects of long-term invasion. Further, I conveyed the importance of Long Point, ON as essential coastal marsh habitat for numerous bird species, including marsh-dependent species in decline throughout Lake Erie and Ontario. I also set the context for my second chapter by discussing current disagreements in the literature regarding *P. australis* impacts on birds within invaded wetlands.

In my 2nd second chapter I built on work by Meyer et al. (2010) carried out during the early stages of invasion (2001 – 2002) in Long Point, Ontario. I surveyed birds in patches of *P. australis,* meadow marsh, and cattail marsh within Long Point's Big Creek National Wildlife Area, Crown Marsh, and Long Point Provincial Park. Additionally, because of the ability of *P. australis* to fill-in open-water pools, I added an evaluation of open-water habitat to the study to fully capture the potential implications of invasion on the different marsh types. In keeping with

the Meyer et al. (2010) study design, I assessed the differences in abundance and species richness among all four vegetation types for both total birds and marsh-nesting birds. I sought to determine if marsh-nesting birds were less diverse and abundant in *P. australis,* if overall bird diversity was lower in *P. australis* patches and if the birds observed in *P. australis* were a subset of birds using meadow marsh and cattail marsh habitat. I found that *P. australis* did not have a significant effect on total bird species richness, or on marsh-nesting bird species richness or abundance, but that birds present in *P. australis,* with the exception of Yellow Warbler (*Dendroica petechia*), were present in higher abundances in other habitat types. In keeping with the historical Meyer et al. (2010) study, I also assessed bird use of the edges of patches (within 50 meters of another vegetation type), hypothesizing that abundance and species richness would be higher in edge stands. However, in 2015 there no longer appeared to be a significant effect of stand location on bird abundance or species richness.

Since invasion may have implications for birds that cannot be captured with simple counts of individuals or species, I also evaluated the species composition of bird communities and bird functional traits (e.g. diet, foraging behaviour, nesting preferences). I sought to determine if the bird species and functional traits of birds supported by *P. australis* were different than other vegetation types, and hypothesized that *P. australis* would support birds that consume insects and nest in shrubs. In Long Point in 2015, *P. australis* did appear to support birds that consumed insects, preferentially nested in shrub habitat, and foraged as foliage gleaners or ground foragers, while birds that hunted via stalking or dabbling, consumed fish, seeds, or plants, and nested on the ground associated with other vegetation types.

In addition to my focus on birds within the marsh, I also characterized the vegetation growing at each point count location, to help evaluate the relationship between vegetation and bird occupancy more thoroughly.

3.3 Implications and Significance

Currently, there is little agreement in the literature regarding whether *P. australis* invasion affects bird communities. My research directly contributes to the improved understanding of the effects of *P. australis* invasion, as it is the only study to compare bird occupancy during the latter stage of *P. australis* invasion with data collected during the early stages of invasion, namely the study by Meyer et al. (2010). Further, my work incorporates a measure of community composition and functional traits to detect subtler effects of invasion than simple changes in species richness and total abundance of birds. My results indicate that community composition must be considered when evaluating the effects of biological invasion.

My findings suggest that the full effects of *P. australis* invasion exhibit a lag time. While the invasion in Long Point appeared relatively benign, or even beneficial for birds in the early stages of invasion (Meyer et al., 2010) when it was expanding exponentially (Wilcox et al., 2003), by 2015 the invasion had seriously altered bird communities. Marsh-nesting species of concern are now excluded from *P. australis* habitat and total bird abundances are lower than found in the historically dominant cattail and meadow marshes. Further, there is no longer any evidence of beneficial edge effects at the margins of *P. australis* patches. These changes are likely due to the progression of *P. australis* invasion. *Phragmites australis* often colonizes new areas by establishment via seed or propagule, and then radiates out from a center point by vegetative reproduction, using stolons, rhizomes and even regrowth from knocked over stems (Kettenring et

al., 2016). The leading edges of expanding patches are less dense, especially in younger stands, but begin to fill in and produce more above-ground biomass and litter as they age (Rooth et al., 2003). In 2001-2002, when the original study found more individuals and species of birds occupying the margins of *P. australis* patches, the sparse stems at the edge of *P. australis* patches may have provided shelter or roosts to birds. Thirteen years later, now that *P. australis* comprises the majority of marsh habitat in our study area in Long Point (Appendix 2), the loss of more diverse cattail, meadow and open-water marsh habitat outweighs any benefits of additional refuge and roosting habitat. Further, the high densities of *P. australis* stems likely makes established *P. australis* patches much less useable for birds: e.g., we observed stem densities of over 70 live stems per m^2 and over 190 stems per m^2 when considering both live and dead stems (Rooney unpublished data). My results suggest that it takes years or even decades for the deleterious effects of *P. australis* invasion to become apparent. This realization helps explain why some studies report finding a significant negative effect of invasion on avifauna, whereas others report negligible effects or even benefits to the bird community: these studies are most likely taking place during different phases of the *P. australis* invasion.

The evaluation of bird species community composition and functional traits also captures significant changes in bird communities between invaded and uninvaded marsh habitat. Examining the relative abundance of bird species is especially pertinent when seeking to capture the effects of *P. australis* invasion on marsh-nesting species of concern that rely on coastal marshes. By analyzing the relative abundance of different bird species and their functional traits, I was able to identify and describe subtler changes occurring in Long Point's avifauna. Although rare throughout Long Point, marsh-nesting species of conservation concern were **never** observed in *P. australis*, and species with functional traits such as ground nesting were more abundant in meadow

and cattail marsh. This exemplifies the need to consider community composition, as a shift from habitat specialists to more generalist species goes unnoticed in simple measures of species richness. Additionally, examining community composition and the functional traits of birds provides a more ecologically meaningful understanding of the changes in bird communities that are resulting from *P. australis* invasion.

These findings are relevant to researchers working with *P. australis,* or wetland managers working in the Great Lakes where *P. australis* invasion is a serious problem, as it threatens biodiversity and species at risk. Furthermore, with climate change and current distribution, *P. australis* is expected to expand its range throughout the Great Lakes (Catling and Mitrow, 2011; Mazur et al., 2014; Tougas-Tellier et al., 2015). This means a thorough understanding of the impacts of invasion on bird communities, and of the tools used to measure changes in biological communities, is timely and relevant to anyone working with *P. australis.* Finally, this work advances our understanding of long-term invasions and also emphasizes the importance of timely, effective control measures to preserve marsh habitat.

3.4 Future Work

More direct measurements of bird use within invaded and uninvaded habitats is the next step in understanding how the *P. australis* invasion is affecting bird use of the Long Point marshes. A measure of nesting frequency and nest success would provide a more in-depth quantification of bird use, whereas work to date has focused simply on bird occupancy. This could also provide insight into the quality of *P. australis* habitat, determining if it presents a viable option for breeding and nesting birds, or an ecological trap and population sink habitat (Pulliam, 1988; Robertson and Hutto, 2006). The work presented in this thesis can help inform future research into the effects of

invasion on bird use, as my thesis highlights which species are abundant in *P. australis* and which were never detected using it.

I also recommend, as suggested by Whyte et al. (2015), that future research examining the ecological effects of *P. australis* invasion seek to characterize *P. australis* habitat more thoroughly, as this would facilitate inter-study comparisons. Approximate stand or invasion age, stem density, canopy height, dominant vegetation species and relative cover within the study system are all variables that could be reported, as they provide relevant detail when interpreting results.

This study is, to my knowledge, the first to repeat an evaluation of bird communities in the same geographical location after many years of invasion progression. This provides a possible explanation for disagreements in the current literature over the severity of *P. australis* invasion effects on bird communities, and fills in knowledge gaps regarding the effects when invasion progresses unimpeded. Further, it fills gaps in the literature regarding the effects of *P. australis* invasion on species composition and functional traits of birds, providing an ecologically relevant measure of effects.

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Appendices

Appendix 1: Photos illustrating the vegetative reproductive characteristics of *Phragmites australis:* A) *P. australis* emergence from a rhizome; B) horizontal rhizome; C) stolons expanding laterally from an established stand; D) a knocked-over stem producing shoots
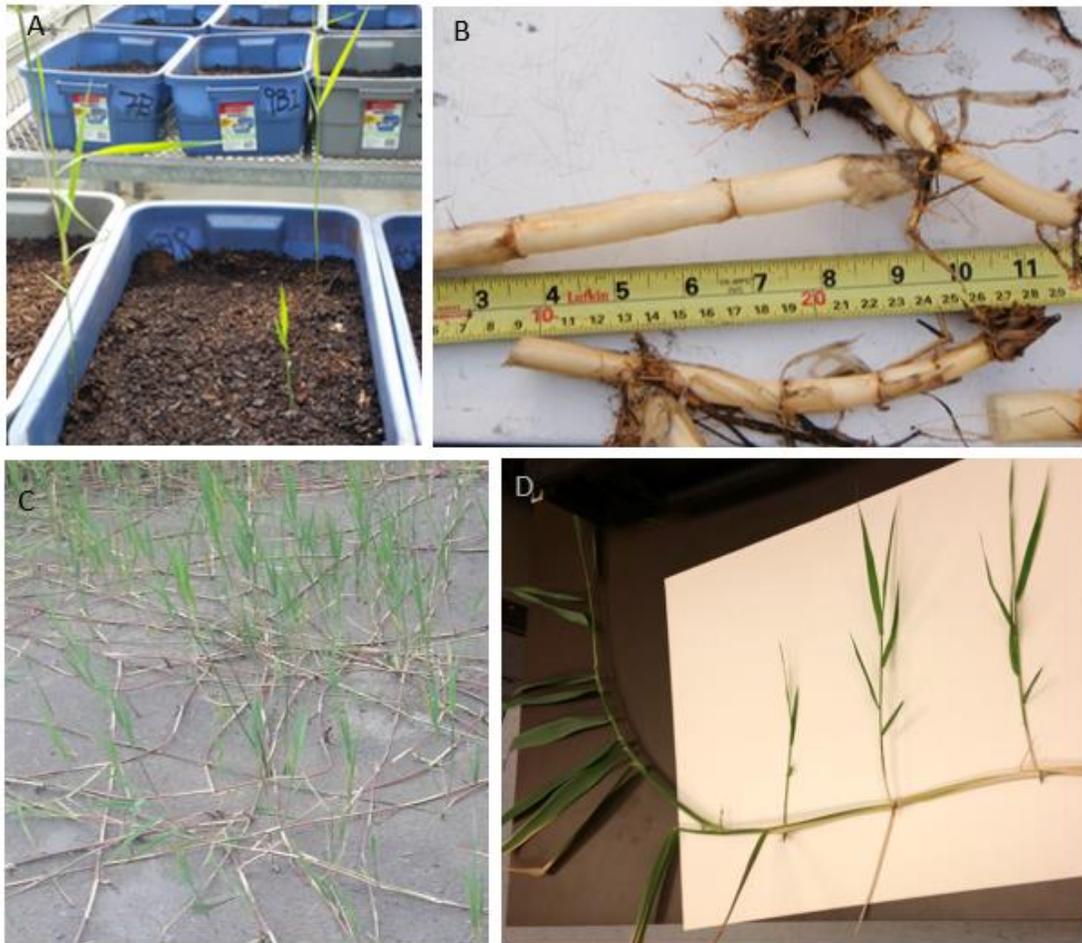
Appendix 2: Extent of *Phragmites australis* land cover in Crown Marsh and Long Point

Provincial Park, Long Point, 2015. Imaging courtesy Ducks Unlimited Canada.
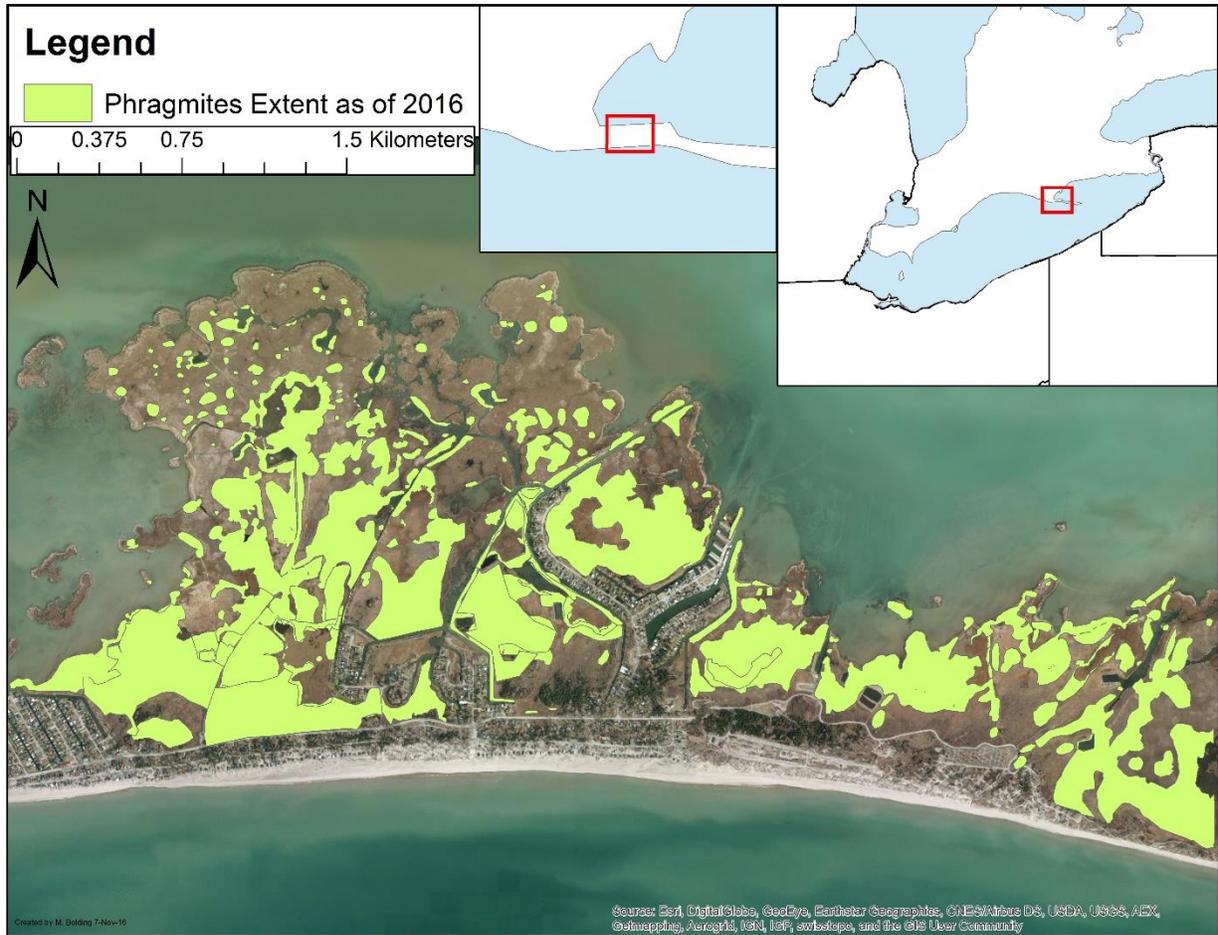
Appendix 3: Photos illustrating the four vegetation types: a) *Phragmitess australis,* b) cattail

marsh, c) meadow marsh, and d) open-water.

Appendix 4: Table 1. All plant and charophyte species identified in August 2015 vegetation surveys at bird point count locations in Long Point, ON using Michigan Flora (Voss and Reznicek, 2012), and verified with the integrated taxonomic information system

Cattail marsh	Meadow marsh	*P. australis*	Open-water
Agrostis stolonifera	*Asclepias syriaca*	*Calamagrostis canadensis*	*Ceratophyllum demersum*
Calamagrostis canadensis	*Aster* spp.	*Calystegia sepium*	*Chara* spp.
Campanula aparinoides	*Calamagrostis canadensis*	*Campanula aparinoides*	*Elodea canadensis*
Carex aquatilis	*Calystegia sepium*	*Carex aquatilis*	*Myrophyllum* spp.
Carex comosa	*Campanula aparinoides*	*Carex comosa*	*Nitella* spp.
Decodon verticillatus	*Carex aquatilis*	*Carex lacustris*	*Nuphar lutea*
Equisetum fluviatile	*Carex buxbaumii*	*Carex lasiocarpa*	*Nymphaea odorata*
Hydrocharis morsus-ranae	*Carex lasiocarpa*	*Carex* spp.	*Pontederia cordata*
Leersia oryzoides	*Carex prasina*	*Cirsium muticum*	*Potamogeton* spp.
Lemna minor	*Carex* spp.	*Cladium mariscus*	*Potamogeton illinoensis*
Lysimachia thyrsiflora	*Chara* spp.	*Cornus stolonifera*	*Potamogeton pectinatus*
***Mentha* spp**.	*Cirsium muticum*	*Decodon verticillatus*	*Sagittaria latifolia*
Nuphar lutea	*Cladium mariscus*	*Helenium autumnale*	*Sagittaria rigida*
***Phragmites australis* (M)**	*Cornus amomum*	*Hydrocharis morsus-ranae*	*Schoenoplectus acutus var. acutus*
***Phragmites australis* subsp**. *americanus*	*Cornus stolonifera*	*Hypericum kalmianum*	*Spirodela polyrrhiza*
Persicaria amphibia	*Decodon verticillatus*	*Impatiens capensis*	*Typha* x *glauca*
Sagittaria latifolia	*Eleocharis smallii*	*Juncus balticus*	*Utricularia* spp.
Sagittaria rigida	*Eleocharis* spp.	*Juncus brevicaudatus*	*Utricularia minor*
***Schoenoplectus acutus* var.** *acutus*	*Epilobium leptophyllum*	*Lemna minor*	*Utricularia vulgaris*
Bolboschoenus fluviatilis	*Epilobium palustre*	*Lycopus* spp.	*Zizania palustris*
***Schoenoplectus pungens* var.** *pungens*	*Helenium autumnale*	*Lysimachia thyrsiflora*	
Spirodela polyrrhiza	*Hydrocharis morsus-ranae*	*Lythrum salicaria*	
Thelypteris palustris	*Hypericum kalmianum*	*Phragmites australis* (M)	

| Cattail marsh	Meadow marsh	*P. australis*	Open-water
Triadenum fraseri	*Juncus brevicaudatus*	*Persicaria amphibia*	
Typha angustifolia	*Juncus arcticus*	*Schoenoplectus pungens* var. *pungens*	
Typha latifolia	*Juncus tenuis*	*Solidago ohioensis*	
Typha* x *glauca	*Lathyrus* spp.	*Solidago uliginosa*	
	Lathyrus palustris	*Spirodela polyrrhiza*	
	Leersia oryzoides	*Stachys palustris*	
	Lemna minor	*Thelypteris palustris*	
	Lycopus uniflorus	*Triadenum fraseri*	
	Lysimachia thyrsiflora	*Typha angustifolia*	
	Lysimachia spp.	*Typha* x *glauca*	
	Lythrum salicaria	*Utricularia intermedia*	
	Mentha spp.		
	Nitella spp.		
	Phragmites australis (M)		
	Persicaria amphibia		
	Potentilla anserina ssp. *anserina*		
	Rosa acicularis		
	Sagittaria latifolia		
	Schoenoplectus pungens var. *pungens*		
	Solidago ohioensis		
	Solidago uliginosa		
	Sorghastrum nutans		
	Spirodela polyrrhiza		
	Stachys palustris		
	Symphyotrichum puniceum		
	Thelypteris palustris		
	Triadenum fraseri		
	Typha latifolia		
	Typha x *glauca*		

Appendix 5: All birds, and their corresponding functional traits, observed during the 2015 Long

Point, ON field season. Marsh-nesting species are indicated with an asterisks (*), and are further

divided into marsh-nesting species of concern ($\pm$)

Common name	Scientific name	Diet	Foraging behavior	Nesting preference
American Bittern*$\pm$	*Botaurus lentiginosus*	Fish	Stalking	Ground
Swamp Sparrow*	*Melospiza georgiana*	Insect	Ground forage	Shrub
Marsh Wren*	*Cistothorus palustris*	Insect	Ground forage	Shrub
Sora*$\pm$	*Porzana carolina*	Seed	Ground forage	Floating
Least Bittern*$\pm$	*Ixobrychus exilis*	Fish	Stalking	Ground
Great Blue Heron	*Ardea herodias*	Fish	Stalking	Tree
Least Sandpiper	*Calidris minutilla*	Insect	Probing	Ground
Virginia Rail*$\pm$	*Rallus limicola*	Insect	Probing	Ground
Common Yellowthroat*	*Geothlypis trichas*	Insect	Foliage glean	Shrub
Red-winged Blackbird	*Agelaius phoeniceus*	Insect	Ground forage	Shrub
Yellow Warbler	*Dendroica petechia*	Insect	Foliage glean	Shrub
Gray Catbird	*Dumetella carolinensis*	Insect	Ground forage	Shrub
Song Sparrow	*Melospiza melodia*	Insect	Ground forage	Shrub
Willow Flycatcher	*Empidonax traillii*	Insect	Flycatcher	Shrub
Tree Swallow	*Tachycineta bicolor*	Insect	Aerial forage	Cavity
Barn Swallow	*Hirundo rustica*	Insect	Aerial forage	Build
Bank Swallow	*Riparia riparia*	Insect	Aerial forage	Burrow
Eastern Kingbird	*Tyrannus tyrannus*	Insect	Flycatcher	Tree
Purple Martin	*Progne subis*	Insect	Aerial forage	Cavity
Chestnut-sided Warbler	*Dendroica pensylvania*	Insect	Foliage glean	Shrub
Downy Woodpecker	*Picoides pubescens*	Insect	Bark forage	Cavity
Common Grackle	*Quiscalus quiscula*	Omnivore	Ground forage	Tree
Canada Goose*	*Branta canadensis*	Seed	Ground forage	Ground
Cliff Swallow	*Petrochelidon pyrrhonota*	Insect	Aerial forage	Cliff
Common Tern	*Sterna hirundo*	Fish	Aerial dive	Ground
Mute Swan	*Cygnus olor*	Plant	Dabbler	Ground
Sandhill Crane*	*Grus canadensis*	Omnivore	Probe	Ground
Wood Duck*	*Aix sponsa*	Insect	Dabbler	Cavity
Blue-winged Teal*	*Chlidonias niger*	Seed	Dabbler	Ground
Mallard*	*Anas platyrhynchos*	Seed	Dabbler	Ground
Caspian Tern	*Hydroprogne caspia*	Fish	Aerial dive	Ground
American Robin	*Turdus migratorius*	Insect	Ground forage	Tree

Appendix 6. Sum of all bird sightings by vegetation type from May – August 2015 in Long Point, ON. Marsh-nesting species are indicated with an asterisks (*), and are further divided into marsh-nesting species of concern (±)

Common name	Scientific name	*P. australis*	Meadow marsh	Cattail marsh	Open-water
American Bittern*±	*Botaurus lentiginosus*	0	0	1	1
Swamp Sparrow*	*Melospiza georgiana*	37	45	53	6
Marsh Wren*	*Cistothorus palustris*	31	25	42	12
Sora*±	*Porzana carolina*	0	2	0	0
Least Bittern*±	*Ixobrychus exilis*	0	1	1	2
Great Blue Heron	*Ardea herodias*	0	0	2	3
Least Sandpiper	*Calidris minutilla*	0	0	0	1
Virginia Rail*±	*Rallus limicola*	0	2	3	1
Common Yellowthroat*	*Geothlypis trichas*	37	35	41	6
Red-winged Blackbird	*Agelaius phoeniceus*	64	95	115	34
Yellow Warbler	*Dendroica petechia*	12	4	2	1
Gray Catbird	*Dumetella carolinensis*	3	0	0	0
Song Sparrow	*Melospiza melodia*	3	11	0	0
Willow Flycatcher	*Empidonax traillii*	1	1	1	0
Tree Swallow	*Tachycineta bicolor*	1	14	3	13
Barn Swallow	*Hirundo rustica*	2	3	0	3
Bank Swallow	*Riparia riparia*	0	2	2	8
Eastern Kingbird	*Tyrannus tyrannus*	2	5	4	0
Purple Martin	*Progne subis*	0	2	0	0
Chestnut-sided Warbler	*Dendroica pensylvania*	0	1	0	0
Downy Woodpecker	*Picoides pubescens*	1	0	0	0
Common Grackle	*Quiscalus quiscula*	0	2	1	0
Canada Goose*	*Branta canadensis*	0	0	0	5
Cliff Swallow	*Petrochelidon pyrrhonota*	0	6	1	3
Common Tern	*Sterna hirundo*	0	0	0	2
Mute Swan	*Cygnus olor*	0	0	0	1
Sandhill Crane*	*Grus canadensis*	0	0	2	1
Wood Duck*	*Aix sponsa*	0	0	0	17
Blue-winged Teal*	*Chlidonias niger*	0	0	0	2
Mallard*	*Anas platyrhynchos*	0	0	0	2
Caspian Tern	*Hydroprogne caspia*	0	0	0	2
American Robin	*Turdus migratorius*	0	1	0	1

Appendix 7: 2D NMS ordination solution of Bray-Curtis dissimilarity matrix calculated using bird species abundances with bird species vectors overlaid (final stress = 22.98). In this joint plot, only species whose abundance was reasonably correlated with at least one ordination axis are depicted as vectors. Symbology of points reflects the three vegetation types considered: *Phragmites australis,* cattail marsh, meadow marsh.
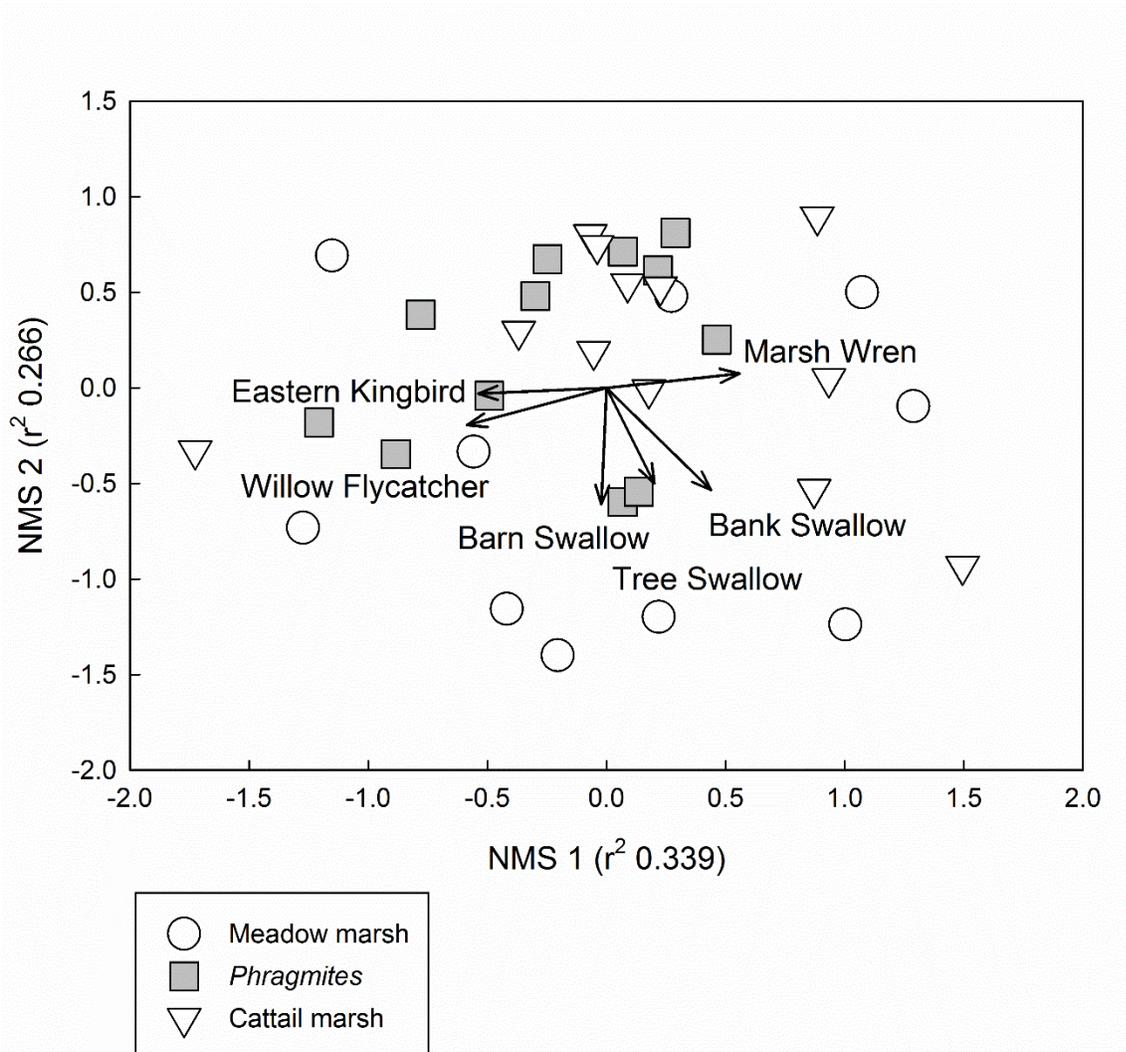
Appendix 8. GPS coordinates and vegetation covariates for all 48 point count locations in Big

Creek National Wildlife Area (BC), Long Point Provincial Park (LP), and Crown Marsh (CM).

All vegetation covariates are based on the average of three quadrats per site. GPS coordinates are

in UTM zone 17.

Site ID	Easting	Northing	Vegetation type	Patch location	Total vegetation cover (%) +/- SD	Dominant species (relative cover %) +/- SD
BC ME1	544824.00	4715225.00	Meadow	Edge	66 (+/- 30)	*Calamagrostis canadensis* 80 (+/- 17)
BC ME2	544655.00	4714303.00	Meadow	Edge	99 (+/- 1)	*Calamagrostis canadensis* 77 (+/- 5)
CM 9	547137.85	4714613.72	Meadow	Edge	20 (+/- 11)	*Cladium mariscus* 35 (+/- 16)
CM 10	546955.29	4714643.33	Meadow	Edge	35 (+/- 4)	*Calamagrostis canadensis* 24 (+/- 6)
LP 12	551332.86	4714520.07	Meadow	Edge	43 (+/- 19)	*Calamagrostis canadensis* 31 (+/- 26)
LP 8R	551023.00	4714879.00	Meadow	Edge	82 (+/- 19)	*Calamagrostis canadensis* 72 (+/- 16)
BC MI1	545148.00	4715205.00	Meadow	Interior	87 (+/- 13)	*Calamagrostis canadensis* 95 (+/- 7)
BC MI2	544956.00	4714585.00	Meadow	Interior	76 (+/- 19)	*Calamagrostis canadensis* 88 (+/- 5)

Site ID	Easting	Northing	Vegetation type	Patch location	Total vegetation cover (%) +/- SD	Dominant species (relative cover %) +/- SD
BC MI3	544483.00	4714504.00	Meadow	Interior	56 (+/- 19)	*Calamagrostis canadensis* 74 (+/- 8)
LP 5	550603.43	4714514.71	Meadow	Interior	33 (+/- 4)	*Calamagrostis canadensis* 20 (+/- 3)
LP 6	551059.78	4714456.36	Meadow	Interior	50 (+/- 6)	*Solidago ohioensis* 27 (+/- 7)
CM MI1	549064.00	4714775.00	Meadow	Interior	18 (+/- 5)	*Calamagrostis canadensis* 18 (+/- 31)
CM 2	547412.43	4714461.36	*Phragmites*	Edge	20 (+/- 3)	*Phragmites australis* 34 (+/- 26)
LP 1	550352.03	4714605.43	*Phragmites*	Edge	56 (+/- 10)	*Phragmites australis* 87 (+/- 15)
LP 9	551334.22	4714335.00	*Phragmites*	Edge	79 (+/- 24)	*Phragmites australis* 18 (+/- 14)
BC PE1	544405.00	4714259.00	*Phragmites*	Edge	85 (+/- 11)	*Phragmites australis* 74 (+/- 35)
BC PE2	544211.00	4714689.00	*Phragmites*	Edge	71 (+/- 17)	*Phragmites australis* 87 (+/- 20)
CM 19	547725.00	4715388.00	*Phragmites*	Edge	47 (+/- 7)	*Phragmites australis* 23 (+/- 6)
CM 6	547661.69	4714678.99	*Phragmites*	Interior	63 (+/- 9)	*Phragmites australis* 97 (+/- 3)
LP 19	550851.46	4714886.68	*Phragmites*	Interior	43 (+/- 9)	*Phragmites australis* 68 (+/- 27)
LP 12R	549727.37	4714787.13	*Phragmites*	Interior	74 (+/- 21)	*Phragmites australis* 95 (+/- 6)

Site ID	Easting	Northing	Vegetation type	Patch location	Total vegetation cover (%) +/- SD	Dominant species (relative cover %) +/- SD
LP 16R	549880.73	4714993.66	*Phragmites*	Interior	66 (+/- 14)	*Phragmites australis* 99 (+/- 2)
BC PI1	543909.00	4714019.00	*Phragmites*	Interior	72 (+/- 13)	*Phragmites australis* 83 (+/- 24)
BC PI2	543954.00	4715651.00	*Phragmites*	Interior	94 (+/- 8)	*Phragmites australis* 100 (+/- 0.02)
BC TE1	545194.00	4715003.00	Cattail	Edge	75 (+/- 7)	*Typha* spp. 21 (+/- 2)
BC TE2	544595.00	4715119.00	Cattail	Edge	59 (+/- 20)	*Typha* spp. 84 (+/- 9)
LP 10	551404.21	4714119.59	Cattail	Edge	45 (+/- 12)	*Typha* spp. 55 (+/- 26)
LP 15	551170.80	4714858.18	Cattail	Edge	42 (+/- 4)	*Typha* spp. 63 (+/- 21)
LP 6R	551443.00	4714845.00	Cattail	Edge	40 (+/- 14)	*Typha* spp. 93 (+/- 9)
BC TI1	544173.00	4715379.00	Cattail	Interior	17 (+/- 3)	*Typha* spp. 88 (+/- 12)
BC TI2	544060.00	4715894.00	Cattail	Interior	48 (+/- 11)	*Typha* spp. 95 (+/- 8)
CM 4R	548166.62	4715395.77	Cattail	Interior	31 (+/- 6)	*Typha* spp. 88 (+/- 8)
CM 5R	548029.83	4715562.28	Cattail	Interior	33 (+/- 0)	*Typha* spp. 100 (+/- 0)
LP 10R	549788.01	4714581.35	Cattail	Edge	52 (+/- 3)	*Typha* spp. 97 (+/- 5)
LP 5R	551696.00	4714961.00	Cattail	Interior	33 (+/- 8)	*Typha* spp. 94 (+/- 11)

Site ID	Easting	Northing	Vegetation type	Patch location	Total vegetation cover (%) +/- SD	Dominant species (relative cover %) +/- SD
LP 7R	551206.69	4715052.17	Cattail	Interior	78 (+/- 24)	*Typha* spp. 44 (+/- 32)
BC OW1	544688.00	4716753.00	Open-water	N/A	33 (+/- 58)	*Typha* spp. 28 (+/- 49)
BC OW2	544572.00	4716439.00	Open-water	N/A	2 (+/- 3)	*Sagittaria rigida* 33 (+/- 58)
BC OW3	545080.00	4714799.00	Open-water	N/A	63 (+/- 26)	*Chara* spp. 54 (+/- 47)
BC OW4	544733.00	4714766.00	Open-water	N/A	85 (+/- 27)	*Nuphar lutea* 31 (+/- 54)
BC OW5	543997.00	4714577.00	Open-water	N/A	40 (+/- 16)	*Nuphar lutea* 78 (+/- 15)
BC OW6	545842.00	4714891.00	Open-water	N/A	98 (+/- 0.8)	*Nymphaea odorata* 78 (+/- 10)
BC OW7	544243.00	4715985.00	Open-water	N/A	100 (+/- 0)	*Potamogeton spp.* 33 (+/- 58)
BC OW8	545285.00	4714682.00	Open-water	N/A	19 (+/- 14)	*Nuphar lutea* 58 (+/- 50)
CM OW1	548937.00	4715056.00	Open-water	N/A	88 (+/- 6)	*Chara* spp. 51 (+/-31)
CM OW2	547562.00	4714960.00	Open-water	N/A	100 (+/- 8)	*Utricularia vulgaris* 56 (+/- 49)
LP OW1	551539.00	4714636.00	Open-water	N/A	77 (+/- 21)	*Nuphar lutea* 43 (+/- 36)
LP OW2	551144.00	4714737.00	Open-water	N/A	67 (+/- 58)	*Chara* spp. 67 (+/- 58)