

Spatially explicit tools to assess
invasion risks by *Phragmites australis*
in freshwater wetlands

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March 2011

A thesis submitted to the Graduate and Postdoctoral Studies Office
in partial fulfillment of the requirements for the degree of
Master of Science

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List of abbreviations

St-François NWA	Lake St-François National Wildlife Area
LULC	Land uses and land covers
GPS	Global positioning system
UTM	Universal transverse Mercator
AUC	Area under the receiver operating curve

Abstract

The rapid progression of an exotic haplotype of common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) in North America is associated with a decline in the plant diversity of wetlands and possibly threatens native haplotypes of *P. australis*. As prevention is a better strategy than control, a spatially-explicit approach was developed to predict the risk of invasion by the exotic *P. australis* and its potential impact on a native haplotype. Focusing on a protected wetland of Quebec, Canada where the two haplotypes occur, this study specifically aimed to: 1) compare and contrast the current spatial distribution of the two haplotypes in relation to landscape and land use/land cover variables, and 2) predict, using spatially-explicit models, the potential expansion patterns of the exotic and native *P. australis*. Results showed that the native *P. australis* was currently more frequent than the exotic *P. australis*. At this stage of invasion, native and exotic *P. australis* still occupied distinct parts of the territory, the native one being associated more with low marsh and areas of lesser human impacts, the exotic one being closer to roads or associated with drier land covers. Perturbations to the natural environment provided invasion foci for the exotic *P. australis* which is more tolerant to disturbances than the native one. The current distribution of invasion foci of exotic *P. australis* and its association to a broad range of conditions resulted in predicted expansion patterns where the cover of the exotic *P. australis* could potentially surpass the cover of the native *P. australis* within 10 years. This could lower the conservation value of the protected wetland and increase the competition with native colonies of *P. australis* where the two haplotypes intersect.

Key words: risk assessment, invasion biology, landscape ecology, ecological modelling, wetlands, *Phragmites australis*, MaxEnt.

Résumé

La progression d'un haplotype exotique du roseau commun (*Phragmites australis* (Cav.) Trin ex Steud.) en Amérique du nord réduit la diversité végétale des milieux humides en plus de menacer les haplotypes indigènes de *P. australis*. La prévention étant plus efficace que le contrôle, une approche spatialement explicite visant à prédire les risques d'invasion par l'haplotype exotique et son impact sur un haplotype indigène a été développée. Cette étude conduite dans un marais protégé du Québec (Canada) visait à : 1) comparer et expliquer la distribution spatiale actuelle de ces deux haplotypes sur la base de leur relation à des variables de couverture/utilisation du sol et du paysage et 2) prédire à partir de modèles spatialement explicites les patrons d'expansion futures des haplotypes exotique et indigène de *P. australis*. À ce stade-ci de l'invasion, les haplotypes occupent des zones distinctes du territoire ; le *P. australis* indigène est associé aux bas marais et à des zones où l'influence anthropique est faible, tandis que le *P. australis* exotique se trouve près des routes et dans les milieux plus secs. Les perturbations au milieu naturel constituent des foyers d'invasion propices à l'haplotype exotique qui semble tolérer un éventail de conditions environnementales plus large que l'haplotype indigène. La modélisation des patrons d'expansion de l'haplotype a démontré que celui-ci pourrait surpasser en couverture l'haplotype indigène d'ici 10 ans, en raison de son association à un vaste éventail de conditions environnementales. Cette progression de l'haplotype exotique pourrait réduire la valeur de conservation du milieu humide et intensifier la compétition avec les colonies indigènes de *P. australis*.

Mots-clés : évaluation du risque, invasion biologique, écologie du paysage, modélisation écologique, milieux humides, *Phragmites australis*, MaxEnt.

Acknowledgments

I would first like to express my sincere gratitude to my supervisor Dr. Sylvie de Blois. Her availability, comments, encouragements and continuous support have been of a great help during these two years and surely contributed to make this experience meaningful. I would also like to acknowledge the work of Erica Haug, Karyne Benjamin and several other students in the Ecolab, who set the basis of this research, as well as the members of the *Phragmites* group for their intellectual input. I must recognize the big help of Dr. Brian Leung and Dr. Martin Jean who provided enlightening comments and helpful feedback. I will surely not forget the interest and enthusiasm of Les amis de la réserve du Lac St-François who kindly let me use their rabaskas. I really appreciated the help of Samuel Turgeon with the construction of cellular automaton models.

A big thank to my labmates, Chaeho Byun, Frieda Beauregard, Laura Boisvert-Marsh, Dominic Chambers, Jean-François Denis, Paola Gomez, Natalie James and Sasha Liston whose support, enthusiasm, and friendship contributed to make these two years at McGill a wonderful experience, and most of all because they kindly accepted to participate to all my crazy projects. Mille mercis à mon père, ma mère, ma tante Christiane, tous les Michel de ma vie, ma grand-mère et mon grand-père pour leur support, leur générosité, leurs précieux conseils, leur attention mais surtout d'être toujours présents dans ma vie. Ma plus sincère gratitude à mes amis qui ont patiemment écouté mes histoires de *Phragmites* et mes nombreuses pratiques de présentation et dont l'humour, l'affection, la gaité et le support me sont chers.

Finally, I would like to thank the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) and the Natural Sciences and Engineering Research Council of Canada (NSERC) for funding my research. Awards provided by the Quebec Center for Biodiversity Science (QCBD), the Department of Plant Sciences, and the Walter M. Stewart fellowship were a great help and allowed me to attend international conferences.

Authors' contribution

Prof. de Blois provided the research questions and funding through grants from FQRNT and NSERC. I collected data, constructed models, interpreted the results, and wrote the thesis, including the first drafts of chapters III and IV, which were edited by Prof. de Blois. Chapter III will be submitted to *Ecoscience* and Chapter IV to *Landscape Ecology*. I presented the results of this study at three international conferences, the 2009 Conference of the International Society for Ecological Modelling, the 24th Conference of the International Congress for Conservation Biology, and the 25th Conference of the International Association of Landscape Ecology.

Chapter I. General Introduction

In the 1960s, an important proportion of wetlands of Canada were drained to create agricultural lands, roads, and residential and commercial areas, as well as to develop the St. Lawrence Seaway. As a result, it is estimated that 70% of wetlands have already been lost or degraded in Canada (Ducks Unlimited 2008). Wetlands are submitted to several stressors and disturbances (e.g., pollution, water level fluctuations and physical alterations) that in turn trigger several negative impacts such as nutrient enrichment, soil compaction, increased sedimentation, and modifications to hydrological cycles (Detenbeck *et al.* 1999). These alterations, combined with a decline of native vegetation, may facilitate the establishment of invasive species (Galatowitsch *et al.* 1999; Zedler and Kercher 2004). In fact, wetlands are among the most invaded systems in the world (Bobbink *et al.* 2006).

In Quebec, the 39 invasive plant species recorded in wetlands of the St. Lawrence River are covering 15 to 18% of wetlands on average (Lavoie *et al.* 2003). Among them, common reed (*Phragmites australis* (Cav.) Trin ex Steud) is probably one of the most aggressive and abundant invaders. Recent genetic analysis showed that the rapid progression of *P. australis* in North America can be attributed to the introduction of an Eurasian haplotype (haplotype M) in the early 19th century (Saltonstall 2002). Studies based on herbarium historical data suggested that this haplotype has been displacing native haplotypes in wetlands of the United States (Lambert and Casagrande 2006). Very few colonies of native *P. australis* seem to remain in Quebec, as 95% of the colonies recorded along roadsides and marshes are exotic (Lelong *et al.* 2007). However, the exotic *P. australis* used to be confined mostly to roadsides (Lelong *et al.* 2007) and linear wetlands (Maheu-Giroux and de Blois 2007), but is now present in several natural wetlands in Quebec (Lavoie 2008). Its presence is generally associated with a decline in native plants' biomass and diversity, as well as a loss of habitat quality and quantity (Chambers *et al.* 1999; Weinstein and Balleto 1999; McGlynn 2009). Moreover, few control methods of the invasive haplotype have proven to be cost effective or free of impact on the native flora (Ailstock *et al.* 2001). There is thus a crucial need to estimate

the risk that the progression of the haplotype may have on the integrity and conservation value of wetlands, and to identify potential threats to the native haplotype.

The general objective of this study was to develop spatially-explicit tools to assess the risk of invasion by the exotic haplotype (M) of *P. australis*, also known as *Phragmites australis* subsp. *australis*, and predict its potential spatial interaction with the native haplotype (F), also known as *Phragmites australis* subsp. *americanus*, focusing on a protected wetland of southern Quebec, Canada. More specifically, the aims were: 1) to compare and contrast the current spatial distribution of the two haplotypes using landscape and land use/land cover variables, and 2) to predict the potential expansion patterns of exotic and native *P. australis* as well as possible areas of overlap between them using spatially-explicit models. This knowledge is provided in the hope that it will help managers of protected areas to estimate better the cost and impacts associated with the progression of the exotic invasive *P. australis*.

In chapter II, the literature on invasive species, on *P. australis*, and on risk assessment methods in invasion biology was reviewed. In chapter III, maps of colonies of exotic and native *P. australis* present in a protected wetland of southern Quebec were used along with redundancy analysis and ANOVA to identify landscape and land-use/land cover variables that can best explain the current spatial distribution of exotic or native colonies. In chapter IV, a habitat suitability model created with MaxEnt, an approach based on maximum entropy, was developed to map the suitable conditions associated with the exotic and native *P. australis* and, combined with data on clonal growth, to predict their potential future distribution in 20 years in the same protected wetland. The approach presented in this study could be adapted to other species to help decide when, where, and how to allocate resources for the control of invasive species in protected areas.

Chapter II. Literature review

Invasive species are a growing concern as their introduction is now more frequent than at any other time before. Vulnerability of protected areas to invasion is exacerbated by several anthropogenic disturbances. In this chapter, the literature on the characteristics and impacts of invasive plant species, on the landscape ecology of invasions, and on risk assessment methods to evaluate the potential impacts of biological invasions was reviewed. The most relevant literature on *P. australis* is also presented.

Biological Invasions

The invaders

Invasions by exotic species are now happening at an unprecedented rate (Ricciardi 2007). The Canadian Wildlife Service defines an invasive plant species as any species « that has moved into a habitat and reproduced so aggressively that it has displaced some of the original components of the vegetative plant community » (White *et al.* 1993). Their spread is often associated with human activities, which enable them to have a wider range of distribution than what they would normally achieve through natural dispersal. Invasive species can be introduced accidentally (e.g., through cars or boats) or intentionally, (e.g., as ornamental plants or for medicinal purposes).

Several investigators tried to find common characteristics of biological invaders (e.g., Hayes and Barry 2008; Moles *et al.* 2008; Whitney and Galber 2008). High dispersal rate, early fruiting, high fecundity, fast growth rate, vegetative reproduction, and tolerance to a wide range of environmental conditions were all characteristics commonly found in invasive plants (Rejmanek 1999; Bobbink *et al.* 2006). However, others showed that there were no pertinent characteristics that separate invasive species from non-invasive species (Goodwin *et al.* 1999), and that predictors of invasibility could vary from one species to another (Daehler 2003). Goodwin *et al.* (1999)

noted that the size of the native range was a more efficient variable to predict invasion success.

According to the Canadian Food Inspection Agency (2008), Canada has 1229 alien vascular plant species. Among them, 486 are recognized as invasive. The majority of introductions occurred during the 19th century. Since the beginning of the 20th century, one invasive plant species is introduced every other year. Half of the introductions are intentional, with the objective to serve as agricultural crops (13% of invasive plant species), ornamental plants (30%), medicinal use (6%), or other usage. Unintentional introduction accounts for 49% of exotic invasive plant species present in Canada. Major pathways of introduction are contaminated plant products such as wood or garden supplies (18% of introduction), livestock (2%), soil (2%), or freight and packed equipment (3%) (Canadian Food Inspection Agency 2008).

The introduction of invasive species into new environments is the second cause of biodiversity loss worldwide, after habitat degradation (Wilcove *et al.* 1998). Wilcove *et al.* (1998) stated that invasive species were one of the main stressors to imperiled species. Yet, Gurevitch and Padilla (2004) affirmed that there is no solid evidence to confirm that invasive species can cause extinctions and suggested that it is the combination of invasion with other stressors (e.g., pollution, habitat destruction) that causes extinctions. Ricciardi (2004) suggested that invasive species can cause extirpations at the population level. Nevertheless, several impacts of invasive species on local diversity and habitat have been documented. Because they compete for space and resources, exotic species may negatively affect native species' richness, although impacts tend to vary with invaders (Hejda *et al.* 2009). Moreover, hybridization between exotic and native species was shown to enhance invasiveness in certain plant species (e.g., *Spartina alterniflora* X *Spartina maritima*, *Mentha aquatica* X *Mentha arvensis*, *Amelanchier humilis* X *Amelanchier* 'clade B') (Ellstrand and Scienrenbeck 2000). Invasive species may also modify habitats for their own benefit, making conditions harsh for local native species that would otherwise be better adapted to their local environment

(Gonzalez *et al.* 2008). The invasive autumn olive, for instance, is reported to increase rates of nitrogen mineralization and nitrification, which could in turn affect underground water quality and slow ecological succession (Goldstein *et al.* 2010).

The costs inherent to invasive species in Canada were estimated in 2006 to reach a total of \$187M (CDN) per year including damages to agriculture, forestry, and fisheries (Colautti *et al.* 2006). Invasive species may also have considerable social impacts, mostly on human health, but also on our appreciation of the environment (Canadian Food Inspection Agency 2008). The problem is also of particular concern in terms of biodiversity protection. In fact, 44 of the plant species at risk in Canada are threatened by invasive species (Canadian Food Inspection Agency 2008). Moreover, invasive species represent an important threat to the integrity of national parks, as they are present in all Canadian parks but Ellesmere Island, and are one of the major causes of changes in species composition (Parks Canada 1998; Keenleyside *et al.* 2006). Invasion is associated with a decrease of the aesthetic and conservation value of some national parks (Keenleyside *et al.* 2006). Exotic invasions are among the five most important stressors to national parks in Canada (Parks Canada 1998).

Vulnerability to invasion

Attempts at identifying common characteristics in all plant invaders were only marginally successful, so other studies tried to predict invasion success based on the characteristics of the invaded habitat or the community. The efficient use hypothesis states that invasive species are more efficient than native ones in capturing light and nutrients, or make a better use of resources (Zedler and Kercher 2004). The enemy release hypothesis suggests that exotic species are more successful in their introduced range of distribution because they are released from predator pressure, unlike native species (Keane and Crawley 2002; Mitchell and Power 2003). The diversity-invasibility hypothesis proposes that more diverse ecosystems tend to be less invaded because they offer a lower availability of resources (Knops *et al.* 1999). However, Van Holle and Simberloff (2005) showed in an experimental design that plant species richness did not

affect invasion success at a small scale. Finally, the fluctuating resource hypothesis states that in period of increased resource availability, competition is decreased and invasions are thus facilitated (Davis *et al.* 2000).

In a review of literature, Theoharides and Duke (2007) found that landscape heterogeneity, size and distribution of suitable habitat patches, and dispersal corridors were all factors that affected the invasion success of exotic species at the landscape level. Principles of island biogeography theory, which describe factors that affect species richness on islands, may be applied to other systems for a better understanding of invasion mechanisms. As such, there are usually more invasive species in small patches than in large patches, and invasive species in large patches are mainly distributed near the edges (Harrison *et al.* 2001; Ehrenfeld 2008). Similarly, at a broader scale, unfragmented landscapes tend to be less invaded than fragmented ones (Primack 2004). This is explained by the fact that the greater the length of contact between a pristine area and adjacent land-uses, the larger the propagule pressure. Propagule pressure is a function of the number of propagules (e.g., rhizome, seeds) released for each introduction, and the number of introductions of invasive species.

Corridors may increase the invasibility of a site by increasing its connectivity with sources of propagules (Parendes and Jones 2000). A study of wetlands in Ontario showed a positive relationship between the number of canals and the density of alien flora (Houlahan *et al.* 2006). Rivers transport seeds, which may later be dispersed through floods (Egertson *et al.* 2004), or rhizomes floating on dead material (Minchinton 2006). Roads can also be linked with the density of invasive species (Tyser and Worley 1992; Lelong *et al.* 2009), although a lag time is often observed between their construction and the arrival of exotic species (Findlay and Bourdages 2000). Roads may also favor invasion by creating new habitats in the roadsides. As they are frequently disturbed by clear-cutting, inputs of de-icing salt, pollutants and dust, roadsides are harsh environments that can only be colonized by disturbance-adapted species (Tyser and Worley 1992; Christen and Matlock 2006). They represent open habitats free of

vegetation and constitute ideal conditions for the establishment of invasive species (Tyser and Worley 1992; Christen and Matlock 2006). Traffic density along roads also seems to have an impact on the density of invasive species. In fact, abandoned roads were reported to be less invaded than used ones (Parendes and Jones 2000). Paths have similar function in facilitating the arrival of invasive species, but to a lesser extent (Usher 1988; Prato and Fagre 2005).

The nature of adjacent land uses may also have considerable impacts on the invasibility of a given site. Propagule pressure has been identified as one of the best predictors of invasibility (Foxcroft *et al.* 2007), even over disturbances or species richness (Van Holle and Simberloff 2005). The nature of land uses surrounding a given site may affect propagule pressure. Research conducted in 302 reserves in the Czech Republic showed that protected areas surrounded by heterogeneous land uses were more invaded than those surrounded by homogenous or pristine lands (Pysek *et al.* 2002). Wetlands surrounded by farms receive more nutrients, which is reported to favor invasive species and allows them to grow faster and form denser colonies (Bertness *et al.* 2002; Bobbink *et al.* 2006). Moreover, habitat patches surrounded by farms are more exposed to propagules than patches surrounded by forest which provide a shade barrier against some invasive species (Theoharides and Dukes 2007). Densities of human populations surrounding a given territory may also influence its invasibility, as more infrastructures are needed to support larger populations (McKinney 2002). Development of infrastructures (e.g., roads, parking, houses) threatens local species that are not adapted to such disturbances and favors tolerant invasive species (DeFries *et al.* 2007; Hansen and DeFries 2007).

Invasive species in wetlands

Wetlands are among the most invaded environments worldwide (Bobbink *et al.* 2006). In the Canadian Great Lakes Region, wetlands within urban and agricultural landscapes are the ones most exposed to several negative impacts such as nutrient enrichment, change in sedimentation rates, modifications of the hydrologic cycles (e.g.

retention time), and soil compaction (Detenbeck *et al.* 1999). Increased nutrient inputs, vegetation removal, and reduced quantity of herbivores were all considered as factors increasing invasive capacities of *Lythrum salicaria*, *Phalaris arundinacea*, *Phragmites australis*, *Typha X glauca* and *Myriophyllum spicatum* in wetlands of North America (Galatowitsch *et al.* 1999). Increased content of P, K and N were correlated with a decrease in plant diversity, as it allows certain species to grow taller, produce more litter, and shade competitors, which leads to the formation of monocultures (Drexler and Bedford 2002). The occurrence of monocultures of exotic species was attributed to high concentrations in nutrients that characterized wetlands located close to farms (Zedler and Kercher 2004). Wetlands with hydrological disturbances are more vulnerable to invasion and are characterized by a decline in diversity of native species (Zedler and Kercher 2004).

Risk assessment

Attempts to control invasive species can be both costly and time consuming. Blossey (1999) pointed out possible negative impacts on local flora and environment induced by some forms of control of invasive species, especially chemical control. Thus, some authors suggested that prevention is often the most cost-effective way to manage invasive species (Thuiller *et al.* 2005). Inglis *et al.* (2006) suggested that eradication and control are easier and more likely to be successful when applied to small and isolated populations. In spite of this, Finnoff *et al.* (2007) observed that managers tend to prefer control over prevention, because control brings direct and measurable results while the outcomes of prevention are less quantifiable. To be able to allocate efficiently limited resources to control or prevent invasions, managers of protected areas need spatially-explicit information about the risks and possible impacts inherent to invasions (Byers *et al.* 2002; Foxcroft *et al.* 2007). Among different foci that risk assessment may have, identifying pathways of introduction is often designated as a crucial one because it enables managers to identify potential sources of propagules (Byers *et al.* 2002; Inglis *et al.* 2006). The estimation of invasion rates also could be a useful way for managers to estimate the costs associated with an invasion (Neubert and Parker 2004).

Habitat suitability models

Ecological niche models, or habitat suitability models, are one of the tools used in the process of risk assessment. These models aim to define a range of suitable conditions for the establishment of a given species by relating occurrence or abundance data with a set of predictors (Pearson 2007). According to Guisan & Thuiller (2005), environmental variables should be chosen in such a way that they include; (1) limiting factors, (2) disturbances, (3) resources. Even though they offer great possibilities for conservation ecology, habitat suitability models still present some limitations. First, these models are based on an equilibrium postulate; they assume that all possible conditions suitable for a species are represented within the set of observations on which the model is based (Guisan and Thuiller 2005). Then, it is taken for granted that the niche is static, and that it will not change with time (Menke *et al.* 2009). Finally, few models take into account biotic interrelations such as competition (Guisan and Thuiller 2005). Nevertheless, habitat suitability models provide a good first approximation of habitat availability and have been used extensively to provide information on probabilities of invasion of exotic species, to project the impact of climate change on species' distribution, as well as to set conservation priorities for endangered species (e.g., Thuiller *et al.* 2005; Crossman and Bass 2008; Evangelista *et al.* 2008).

Phragmites australis

Distribution

Phragmites australis (Cav.) Trin. ex Steud. (hereafter referred to as *P. australis*) is a tall perennial emergent angiosperm that grows in salt, brackish and freshwater marshes but also in swamps and ditches (Haslam 1972; Mal and Narine 2004; Maheu-Giroux and de Blois 2007). Present on all continents but Antarctica, *P. australis* is one of the most widespread angiosperms in the world (Mal and Narine 2004). The species is most frequent in temperate regions, but is also found in tropical climates except for the Amazon Basin.

Ecology/Biology

The ability of *P. australis* to colonize new environments and form monotypic colonies was partially associated to its tolerance to variation in environmental conditions. The species can tolerate salinity level up to 41 (based on a dimensionless conductivity ratio), but the rate of growth is slowed when salinity exceeds 26 (Sun *et al.* 2007). *P. australis* can adjust its water and cation loss to face higher soil salinities (Lissner *et al.* 1997). It is usually found at pH from 5.5 to 8.1, but can also be found in more acidic conditions (pH 4.4 to 4.8) (Hocking 1989; Mal and Narine 2004). *P. australis* can be found in soil with organic matter contents varying from 1 to 97% (Haslam 1972). The species benefits from increased nutrient availability which enables it to produce more biomass, shoots, and rhizomes, and thus allows it to shade more successfully its competitors (Bertness *et al.* 2002; Minchinton and Bertness 2003; Ravit *et al.* 2007; Kettenring and Whigham 2009). The response to increased nutrient levels can be observed over more than one growing season as the species shows a good capacity to store nutrients (Minchinton and Bertness 2003). Consequently, a positive correlation between the presence of agricultural lands and the density of *P. australis* was found by Trebitz and Taylor (2007) and Chambers *et al.* (2008). Roadsides also provide suitable habitats for the establishment of colonies of *P. australis*. In southern Quebec, the probability of finding a colony increases with the proximity to a road, and is higher near larger roads (Lelong *et al.* 2009). It was shown that *P. australis* has a competitive advantage over *Typha spp.* in situations of increased salinity (Paradis 2008). *P. australis* is also frequent in disturbed areas (Minchinton and Bertness 2003; Wilcox *et al.* 2003). Vegetation removal was shown to increase the ability of *P. australis* to spread into new territories (Minchinton and Bertness 2003) as it creates favorable conditions for seed establishment (McCormick *et al.* 2010). *P. australis*' invasion potential was also attributed to its high plasticity. The size of clones, shape of leaves, and density and diameter of stems may all vary with habitat alteration or competition (Mal and Narine 2004; Bellavance 2006).

Limitations

One of the main factors limiting the spread of *P. australis* is water level (Wilcox *et al.* 2003; Hudon *et al.* 2005). Propagation is faster and more efficient when water levels are lower than 1 meter (Bart and Hartman 2000; Alvarez *et al.* 2005; Hudon *et al.* 2005; Tulbure and Johnston 2010). The species is also tolerant to long term droughts through which it adapts by modulating leaf area (Pagter *et al.* 2005).

Phragmites australis uses both sexual and vegetative (above and belowground) reproduction (Mal and Narine 2004). Recent genetic analyses of *P. australis*' patches in Rhode Island (McCormick *et al.* 2010) and Great Lake St-François (Belzile *et al.* 2010) suggest that the species uses primarily seed dispersion to establish into new environments. Expansion of existing colonies is achieved mostly through clonal reproduction (Hudon *et al.* 2005; Belzile *et al.* 2010); although seed recruitment is also used to expand (McCormick *et al.* 2010). Wind, flood, and birds would be major vectors by which seeds of *P. australis* disperse (Small and Catling 2001). Seed viability of 3 to 7% was observed by Maheu-Giroux and de Blois (2007) in southern Quebec, although Mal and Narine (2004) noted that seed viability is extremely variable within populations. An inverse correlation was found between foliar concentration in nitrogen and phosphorus and seed viability (Kettenring and Whigham 2009). Seed establishment is reported to be more successful on bare humid soil (Mal and Narine 2004). McCormick *et al.* (2010) showed that establishment of new colonies through seed recruitment was faster in sites dominated by human activities than in undisturbed sites. Frosts, flooding, and droughts are reported to affect growth and survival of seedlings (Haslam 1972; Mal and Narine 2004). Germination is also jeopardized in saturated soil or under high vegetative cover (Mal and Narine 2004). Fragments of rhizomes generally show better survival rates than seeds; they can survive under vegetated cover and on burned or bare soils (Ailstock *et al.* 2001). Survivorship of rhizomes seems to be optimal when buried, especially in salt marshes where burying prevents desiccation (Bart and Hartman 2000; Ailstock *et al.* 2001). Thus, transport of rhizomes through machinery during road construction is an

ideal vector for the implantation of *P. australis* rhizomes (Gervais *et al.* 1993; Ailstock *et al.* 2001).

Haplotypes

At least two haplotypes of *P. australis* are currently found in Quebec, an exotic one (*Phragmites australis* subsp. *australis*) and a native one (*Phragmites australis* subsp. *americanus*) (Lelong *et al.* 2007). These two haplotypes are visually distinguishable through the color of their stems (red for the native haplotype, green for the exotic *P. australis*), and the width of their inflorescences (larger for the exotic *P. australis*) and leaves (larger for the exotic *P. australis*). The oldest colony of exotic *P. australis* was dated back to 1916 in the herbarium records and was found in the Chaudière-Appalache region (Lavoie *et al.* 2003). Until the 1970s, exotic *P. australis* remained scarce, while the majority of colonies of *P. australis* in Quebec were native. The expansion of the road network in southern Quebec and low water levels in the St. Lawrence River allowed for a rapid progression of the exotic haplotype in the 1970s (Gervais *et al.* 1993; Lelong *et al.* 2007). Nowadays, the exotic haplotype is largely dominant in the province; 95% of all colonies sampled in Quebec and 99% of colonies located along roadsides are exotic (Lelong *et al.* 2007). Twenty-six colonies of native *P. australis* have been identified and are largely confined to natural wetlands. These colonies are found near Lake St-François and Lake St-Pierre, in the Saguenay, in the Bas St-Laurent, and in the Gaspésie regions (Lelong *et al.* 2007). The exotic haplotype is very abundant near roads and in linear wetlands (e.g., drainage ditches) (Lelong *et al.* 2007; Maheu-Giroux and de Blois 2007). The exotic haplotype seems to be using these corridors to invade natural wetlands. It is now present in a dozen natural wetlands, but is still mostly confined to the shore of the St. Lawrence River (Lavoie 2008). Studies based on herbarium historical data implied that the exotic haplotype could have been displacing native haplotypes in wetlands of the United States, although direct interactions have not been documented (Saltonstall 2002; Lambert and Casagrande 2006).

For a long time, it was thought that the two haplotypes of *P. australis* could not hybridize because they were blooming and senescing at different time. However, recent greenhouse experiments demonstrated that exotic and native *P. australis* can hybridize and produce viable seedlings (Meyerson *et al.* 2010). Hybrids were also found growing in the Great Lakes region (Paul *et al.* 2010), the only field report of hybrids so far.

As the discovery of an exotic haplotype is fairly recent (Saltonstall 2002), differences between native and exotic haplotypes have been poorly studied. The majority of studies focused on morphological differences, and very few of them were done at the landscape level. It was shown that the exotic haplotype has a greater density of stems and leaves, and greater biomass than its native counterpart (League *et al.* 2006; Modzer and Zieman 2010). Higher concentrations of chlorophyll in the exotic haplotype suggests that it can sustain greater rates of photosynthesis, but would need more sunlight to do so (Modzer and Zieman 2010). The exotic reed is also characterized by higher contents of nitrate, although it is unclear whether this reflects its distribution in mostly disturbed areas or a greater need for nutrients (Packett and Chambers 2006; Modzer and Zieman 2010). It was also shown that the exotic reed has higher nutrient uptake rates which enables it to exploit nutrients pools more rapidly (Modzer and Zieman 2010). The exotic *P. australis* is also more tolerant to higher salinity concentrations than the native one, as it can produce more shoots and sustain a higher growth rate under increased salinity levels (Vasquez *et al.* 2005).

Effects on biodiversity and habitat

The exotic *P. australis* is reported to reduce the overall biodiversity and quality of the habitats and ecosystems that it invades (Chambers *et al.* 1999; Warren *et al.* 2001). The plant forms vast and dense monotypic stands, which are correlated with a reduction of the biomass, richness, and abundance of other plant species (Chambers *et al.* 1999; Warren *et al.* 2001; McGlynn 2009). Studies showed that *P. australis* has a competitive advantage over *Spartina alterniflora*, *Lythrum salicaria* and *Typha angustifolia* (Burdick and Konisky 2003). The massive production of slowly decomposing litter by mature

stands of *P. australis* limits seed germination and seedling establishment of other species (Haslam 1972). Its early emergence also provides an advantage as it allows *P. australis* to benefit rapidly from sunlight and shade its competitors (Farnsworth and Meyerson 2003; Osgood *et al.* 2003). As *P. australis* produces a lot of slow decomposing litter and is characterized by high evapotranspiration rates, marshes that it invades show an increased peat compaction as well as a diminution of the water table level (Osgood *et al.* 2003). This increase in litter and organic matter content results in a greater deposition of sediments, and eventually, a higher elevation of marshes and a reduction of the density of drainage channels (Weinstein and Balleto 1999; Osgood *et al.* 2003; Rooth *et al.* 2003). It could also affect larval and juvenile fish, whose mobility is compromised by the accumulation of litter and sediments in creeks (Chambers *et al.* 1999; Warren *et al.* 2001). Effects on mature fish seem to vary; a decrease of resident fish was observed by Hunter *et al.* (2006) whereas Osgood *et al.* (2003) observed that some fish populations used *P. australis* colonies. A decrease of the overall diversity of birds in marshes invaded by *P. australis* was observed by Chambers *et al.* (1999). Benoit and Askins (1999) noted a lower diversity of bird species in *P. australis*' communities than in meadows, as mixed vegetation stands often provide better breeding environments than tall monotypic stands of emergent species. Finally, ecosystems colonized by *P. australis* are reported to experience a decrease in the diversity of habitats (Chambers 1999; Mal and Narine 2004).

Control

Even though several methods of control of *P. australis* have been studied, few showed cost-effective results. Ailstock *et al.* (2001) tested both herbicide and burn-herbicide treatments in non-tidal wetlands. An increase in plant diversity was rapidly observed after the treatment, but *P. australis* was reported to re-colonize after 3 years. Thus, to be efficient, herbicide treatments would need to be repeated every 2 to 3 years, which could meanwhile jeopardize the surrounding vegetation (Blossey 1999). Harvesting a colony of *P. australis* may reduce its mean aerial and aboveground biomass, but is rapidly followed by an increase in stem density. Burn treatments have a

minimal effect (Asaeda *et al.* 2006). A successful control of the species may be achieved through a modification of hydraulic conditions; an increase of the water level of 1 to 2m, or a continuous inundation during 100 days, is reported to impede the progression of the species (Hudon *et al.* 2005). In a review of the literature, Tewksbury *et al.* found 26 herbivores that fed on *P. australis* in North America. Only five were native (e.g., *Ochlodes yuma*, *Calamomyia phragmites*, *Poanes viator*), 16 recently introduced (e.g., *Rhiezadra lutosa*, *Apamea unanimitis*), and the status of five more was unknown. Experiments showed that the attacks of European *Archanara geminipuncta* on exotic *P. australis*' stands were effectively reducing flowering, stems' height, and aboveground biomass (Haefliger *et al.* 2006). However, authors were not yet able to tell whether this herbivore would have detrimental effect also on the native haplotype. Lambert *et al.* (2007) noted that two species of *Liparia* (*Liparia similis* Schiner and *Liparia rufitarsis* Loew) were negatively affecting stems' length and that the attacked stems were not flowering. However, these authors also reported that the native *P. australis* was more attacked by the *Liparia* species than was the exotic *P. australis*.

Although *P. australis* has been extensively studied, this literature review reveals a critical need for better options regarding the management strategies of *P. australis* in protected areas, where traditional control methods (e.g., herbicide treatments, flooding) cannot be applied without considerable impact on the surrounding vegetation and the integrity of habitats. Moreover, it has been shown in this chapter that, as the discovery of the exotic haplotype of reed is fairly recent, few studies have been dedicated to comparing the distribution of the exotic and native *P. australis* in the same area. Knowledge on their current and potential future distribution is nevertheless critical when wanting to control one while protecting the other.

Chapter III

Comparing the spatial distribution of two haplotypes of common reed (*Phragmites australis*) in a freshwater wetland*

Sophie Taddeo and Sylvie de Blois

Abstract

When entering new ecosystems, invasive exotic species may have many detrimental impacts, especially on native congeners potentially sharing common ecological requirements. Explaining the spatial distribution of two related species provides useful insights on the specific conditions in which they each occur and their potential to overlap and compete. The objective of the study was to use landscape and land use/land cover variables to compare and contrast the spatial distribution of colonies of exotic and native common reed (*Phragmites australis*) co-occurring in a protected freshwater wetland. Results showed that the protected area served as a refuge for the native *P. australis* which is found at higher frequency than the exotic type. At this stage of invasion, native and exotic *P. australis* still occupied distinct parts of the territory, the native one being associated more with low marsh and areas of lesser human impacts, the exotic one being closer to roads or associated with drier land covers. Perturbations (roads, human-made canals, human settlements) to the natural environment provided invasion foci for the exotic *P. australis*. As the exotic *P. australis* seemed tolerant to a broader range of environmental conditions compared to the native one, this suggested that disturbances to a given land cover may be more important in creating invasion foci than the nature of the land cover itself.

* Manuscript for submission to *Ecoscience*

Introduction

When entering new ecosystems, invasive species have detrimental impacts on native species and on habitat quality. Invasive species act in synergy with other stressors to affect native species, even causing extirpations at the population level (Gurevitch and Padilla 2004; Ricciardi 2004). Invasive species can affect native species by introducing new diseases or by competing for space and resources (D'Antonio and Meyerson 2002). These species can also impact the quality, the diversity, and the ecological functions of habitats as they may modify ecosystems to their own benefits, thus threatening native species and facilitating the arrival of other noxious species (Petillon *et al.* 2005; Gonzalez *et al.* 2008; Miehl *et al.* 2009).

The introduction of an invasive species may be particularly problematic where a related native species is found. If these related species are sharing common ecological requirements, there is a greater chance that one will have a detrimental effect over the other (Thum and Lennon 2010). The species with a superior capacity to function with limited resources or a superior capacity to access these resources will often be more competitive and dominant (Vermeulen *et al.* 2009). Furthermore, impacts could be worse if these species were to hybridize, as is common for plants. Hybridization was found to be a factor enhancing the invasion potential of certain plant species (Ellstrand and Scienrenbeck 2000; Zalapa *et al.* 2010). Studying the extent to which the niches of two closely related species overlap may provide useful information to determine whether the intruder poses real risks to related species (Byers *et al.* 2002; Thum and Lennon 2010).

In this study, the spatial distribution of two haplotypes of common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), an Eurasian and invasive one (*Phragmites australis* subsp. *australis*) and a native one (*Phragmites australis* subsp. *americanus*), were compared. The exotic *P. australis* was introduced in North America at the beginning of the 19th century. In southern Quebec, it experienced an astonishing progression during the 1970s, favored by the extension of the road network, low water

levels in the St. Lawrence Seaway, and the disturbance of several natural wetlands (Lavoie *et al.* 2003; Lelong *et al.* 2007). The exotic *P. australis* is now widely distributed along the major roads and highways of southern Quebec (Jodoin *et al.* 2008), is progressing in linear wetlands (Maheu-Giroux and de Blois 2007), and is starting to spread in natural wetlands (Lavoie 2008).

Herbarium data suggest that the exotic haplotype could have been displacing native populations in marshes of the United States, although direct interactions have never been observed (Lambert and Casagrande 2006). Recent laboratory and field evidence showed that the two haplotypes can successfully hybridize, which could lead to a more aggressive hybrid and cause genetic pollution of the native strain (Meyerson 2007; Meyerson *et al.* 2010; Paul *et al.* 2010). As the similarities and differences between these haplotypes have been studied mostly at the population level (Vasquez *et al.* 2005; League *et al.* 2006; Packett and Chambers 2006; Modzer and Ziemann 2010), there is a crucial need for studies that would enhance our comprehension of their respective patterns of distribution at the landscape scale. The overall objective of the study was to identify landscape and land uses/land covers variables that explain the spatial distribution of an exotic haplotype of *P. australis* and a native one in a protected wetland.

Methods

Study site

The study area is located at the Lake St-François National Wildlife Area (hereafter referred to as St-François NWA; 45° 01' N , 74° 30' W), a federally protected reserve since 1978 located on the south shore of Lake St-François at the border between the state of New York, USA and the province of Quebec, Canada (Figure 3.1). Lake St-François, located between Cornwall, Ontario (45° 01' N , 74° 45' W) and Salaberry-de-Valleyfield, Quebec (45° 15' N , 74° 08' W), is a natural opening of the St. Lawrence River. The St-François NWA comprises 1347 hectares (Ministère du développement durable, de l'environnement et des parcs du Québec 2009). In 1987, it was conferred

RAMSAR status as an internationally remarkable wetland and one of the last large remaining expanses of freshwater wetlands in the agriculturally dominated area of southern Quebec. The St-François NWA is situated within the hardwood forest subzone, in the sugar maple bitternut domain (Ministère des ressources naturelles du Québec 2003) and is surrounded by agricultural land with corn fields or wet meadows and some low density housing (Maheu-Giroux *et al.* 2006). Climate is cool temperate with average annual temperature of 6.5°C and average annual precipitation of 944.8 mm (Environment Canada 2009). The St-François NWA comprises several community types, including swamps dominated by shrubs such as *Alnus incana* subsp. *rugosa* (considered invasive), low marsh dominated by *Carex spp.*, *Sparganium eurycarpum* and *Typha spp.*, high marsh dominated by *Carex spp.*, forest patches and aquatic communities (Létourneau and Jean 2006).

Although protected, the ecosystems of the St-François NWA, as most wetlands around the world, have been under increased pressures from human activities. First, the modification of the hydrological regime of Lake St-François between 1940 and 1970 for various purposes has resulted in an overall increase in mean water level and a relative stabilization of annual variation in water level compared to previous conditions (Auclair *et al.* 1973). Second, human-made fires have been occurring in the St-François NWA up to the 1970s, as evidenced by field observations and the analysis of aerial photographs (Jean and Bouchard 1993; Maheu-Giroux *et al.* 2006). With the cessation of fire, large areas of the St-François NWA previously covered by *Carex spp.*-dominated marshes have been invaded by *Alnus incana* subsp. *rugosa* (Jean and Bouchard 1991). Third, agricultural activities around the St-François NWA have greatly intensified in the last four decades following changes in agricultural policies and the construction of a vast network of agricultural drainage ditches to drain the rich clay soil of the region (Domon and Bouchard 2007). At some locations and because of the slope patterns, agricultural lands are being drained into watercourses flowing through the St-François NWA. Fourth, Ducks Unlimited Canada has conducted in the 1980s work that involved digging and dredging for the creation of a network of channels to manage waterfowl use within the

St-François NWA. Finally, roads and trails make some parts of the St-François NWA more accessible than others, introducing disturbances. All these changes have undoubtedly affected vegetation patterns and may have contributed to increase vulnerability to invasive species, but this has received little attention.

Data collection and mapping

The locations of all colonies (181) of *P. australis* in the St-François NWA were identified during summer and winter of two sampling seasons (2006-2007), and their boundaries recorded using a GPS receiver mobile mapper. The haplotype was identified in the field through morphological differences (red stems, narrow leaves, small inflorescence for the native *P. australis*; green stems, wider leaves and larger inflorescence for the exotic *P. australis*). DNA analysis was performed by Annie St-Louis at the Phytologie Department of Laval University in 2006 on 65 random leaf samples (37 native and 28 exotic) following the methodology of Saltonstall (2002) to validate field identification. There was 100% agreement with the field classification.

The spatial coordinates of the colonies were imported as an ArcView shapefile onto a base map of the St-François NWA, using the Universal Transverse Projection of Mercator, zone 18. The base map included different features such as roads, bodies of water, canals, dykes, and land uses/land covers (LULC) present in the study site. These features were identified through field surveys, aerial photographs, and thematic maps. National road, Lake St-François, rivers, and human-made canals were mapped by screen-digitizing aerial photographs. The positions of secondary roads and dykes were obtained in the field, using the 'create a line' function of a GPS receiver mobile mapper.

A grid of 25m² cells was created to cover the whole study area for analysis. The "polygon in polygon analysis" function of Hawth's tool 3.27, implemented in ArcGIS 9.3 was used to estimate the % cover of *P. australis* in each cell. *P. australis* was considered present when it covered at least 25% of a 25m² cell. In total, 6069 cells with cover records (2234 for exotic *P. australis* and 3835 for native *P. australis*, two of which had also the exotic one) were used for statistical analyses. Cells with no *P. australis* were not

included as the focus was on comparing the conditions associated with the two haplotypes.

Four environmental variables were obtained from the base map and used to perform the analyses. These explanatory variables were: 1) distance to the nearest road (0 – 1500 m), which includes a national road as well as some secondary roads, 2) distance to natural bodies of water (0 m – 1450 m), which includes Lake St-François and three natural rivers, 3) distance to dyke and canals (0 m – 2200 m), which includes human-made canals used to drain adjacent farms or canals for waterfowl habitat, and 4) land use and land cover (LULC). The LULC classification was based on a map by Létourneau and Jean (2006) of wetlands located on the shore of Lake St-François using images taken by the remote sensing satellite Ikonos between July, 25 and August, 21 2002, with a scale of 1:50 000 and a precision of around 15 to 25 meters (see table 3.1 for a description of the categories of LULC). The Zonal Statistic ++ tool of Hawth's toolbox implemented in ArcGIS 9.3 was used to determine categories of land use or land cover in cells. The Euclidean distance function of the Spatial Analyst Tool implemented in ArcGIS 9.3 was used to measure the Euclidean distance from the centroid of a cell to a given feature.

Statistical analysis

A redundancy analysis was conducted using the abundance (cover) of native or exotic *P. australis* as the response variables to identify the set of explanatory variables that discriminated between sites occupied by one or the other haplotype. Explanatory variables (i.e., distance measures) were standardized to facilitate their comparison. Nominal variables (LULC) were treated as binary variables. A forward selection was applied with the `forward.sel` function of the `packfor` library implemented in R 2.8.1, to keep only variables that had a significant incidence ($R^2 > 0.001$) on the response variable. Statistical significance of the canonical relation between response and explanatory variables and statistical significance of each canonical axis were both verified with a permutation test ($n=9999$).

A contingency table was built for each set of explanatory variables (distance variables and LULC) to determine which distances and which LULC best accounted for the difference between the cells occupied by either one or the other *P. australis*. A Pearson's chi-squared test was performed through the function `chisq.test` implemented in R 2.8.1, to test for the independence of the response variables. A Freeman-Tukey test was then conducted to test the statistical significance of the difference between observed values and expected values (i.e., obtained by multiplying the sum of a row by the sum of a column and dividing it by the total). The statistic is computed as follows;

$$X^2 = \frac{(O - E)}{\sqrt{E}}$$

where *O* is the observed value, and *E* is the expected value. Observed values are considered significantly different from expected values when their absolute value is larger than a critical value, computed by dividing the corresponding chi statistics by the number of cells in the contingency table.

Results

Native *P. australis* is currently more abundant in the St-François NWA than exotic *P. australis*. In 2006, it covered 116 157 m² whereas exotic *P. australis* covered 79 176 m². The canonical combination of explanatory variables from redundancy analysis explained 46.4% of the variation in the cover records of the exotic and native *P. australis* (Table 3.2). The canonical relation between response and explanatory variables was significant ($p = 0.001$), as was the first axis only (97% of variance). Both "distance to road" and "distance to natural bodies of water" were retained as variables discriminating between cells occupied by exotic or native *P. australis*, whereas the "distance to dyke and canals" variable was not. Among all LULC, built-up areas, farms, ploughed lands, dry meadows, forested swamps, fallow lands dominated by *Rhus typhina*, high marshes, fallow lands dominated by *Crataegus spp.*, high marshes dominated by *Carex spp.*, and low marshes dominated by *Zizania spp.* were all retained as significant variables discriminating between cells occupied by the exotic *P. australis*

from cells occupied by native *P. australis*. The exotic *P. australis* was positively correlated to the first axis, whereas native *P. australis* was negatively correlated to it (Table 3.2). The variable “distance to roads” was negatively correlated to the first axis, implying that native *P. australis* was generally found at greater distances to roads than exotic *P. australis*. Exotic *P. australis* was more frequently associated with built-up areas, farms, and high marshes, as these LULC were strongly correlated with axis 1.

Freeman-Tukey deviates showed that the exotic *P. australis* was more frequent than the expected value on anthropogenic land-uses such as built-up area, fallow land dominated by *Crataegus sp.*, fallow land dominated by *Rhus typhina*, farms, and ploughed land, whereas the native *P. australis* was less frequent than expected on these land-uses (Table 3.3). Fallow land dominated by *Populus balsamifera* was the only land use where native *P. australis* was more represented than expected.

Native *P. australis* was more frequent than expected in three out of five classes of low marshes and one out of three classes of shrub swamps, the one dominated by *Alnus incana* subsp. *rugosa* (Table 3.3), which is the dominant land cover in the St-François NWA. Among the three classes of high marshes, only the general class “High marsh” (i.e. high marshes where no species was identified as dominant) was significant and related to higher than expected frequency of exotic *P. australis*. Two of the four forested swamps classes, those dominated by *Fraxinus pennsylvanica* and those with no dominant species, were significantly associated with higher frequency of exotic *P. australis*. Finally, no class of forests was retained as significant in the analysis.

Exotic *P. australis* was more frequent than expected when located at less than 50m of a road, at 550m, and at 950m away from it, whereas native *P. australis* was significantly more frequent than expected further away from roads, from 150 to 350m, 450 to 600m and 1000 to 1500m (Table 3.4). Neither haplotypes were found at distances to roads greater than 1500 meters. Native *P. australis* was more frequent than expected in cells located less than 50m or at 450m away from natural bodies of water. Exotic *P. australis* was more frequent in all other significant classes (Table 3.4).

Discussion

Native *P. australis* is currently more abundant in the St-François NWA than exotic *P. australis*. It is unclear what the historical distributions of the haplotypes were in the St-François NWA, as the identification of an exotic haplotype is fairly recent in North America (Saltonstall 2002), but it is likely that the exotic haplotype has been recently introduced there as elsewhere in Quebec. In a study of vegetation communities of the region, Auclair *et al.* (1973) observed that, when present, *P. australis* was dominant in emergent communities (99.9% of dry material), but only accounted for 10.9% of dry material of meadow communities. Auclair *et al.* (1976) observed a maximum biomass production of *P. australis* in plots where water levels were around 1m. Based on our current knowledge of *P. australis*' spatial distribution, it would appear that the native haplotype was the most likely to have been sampled in those studies. The native haplotype was observed near bodies of water, whereas the exotic haplotype is not as tolerant of high levels of water (Hudon *et al.* 2005; Meadows and Saltonstall 2007). Moreover, Jean and Bouchard (1993) in a report on vegetation patterns along riparian systems of the same area recorded 96 species from sampling done in 1986-1987, but surprisingly there is no mention of *P. australis* (complete list of species not included in their study). A vegetation survey conducted in 2000 by Environment Canada (Létourneau and Jean 2006) mainly to validate the mapping of vegetation classes gathered from satellite imagery reported 2 out of 37 quadrats with *P. australis* present. Current observations in the field suggest that these were probably exotic *P. australis*. It is thus likely that exotic and native *P. australis*' populations are at different stages of their progression in the territory. This situation may limit comparison between their spatial distributions, the exotic reed having not yet filled its niche. Nevertheless, the results provide information about invasion foci of exotic *P. australis* in the St-François NWA as well as insights about conditions in which both haplotypes can be found and therefore potentially compete.

Results showed that the current distribution patterns of the exotic and native reed were mainly explained by their spatial relationships to roads, natural bodies of

water, and anthropogenic land-uses. Exotic *P. australis* was more frequent near roads and near anthropogenic land covers such as farms, fallow lands, and built-up areas than native *P. australis* was. Native *P. australis* was poorly represented in these land uses, but it was more frequent at short distances to natural bodies of water where the exotic *P. australis* was still scarce.

The majority (90%) of cells occupied by the exotic *P. australis* were found at less than 50m from a road. Although exotic *P. australis* is dominant at these distances, 50% of cells occupied by native *P. australis* were also found within the same distances. However, native reed's colonies were only found close to low traffic secondary roads and were more frequent than the exotic reed when located further than 450 meters away from a road. Our results are similar to what was observed at the regional scale by Jodoin *et al.* (2008) who found that 99% of the colonies found in ditches of highways in Quebec were exotic, but did not study the distribution of *P. australis* along secondary roads. Lelong *et al.* (2009), however, found the probability of presence of exotic *P. australis* to increase with the importance of the road.

Genetic analyses of exotic *P. australis*' populations and evidence from spatial patterns of invasion in linear habitats suggest that seed dispersal is responsible for *P. australis*' establishment in new sites more than what was previously thought (Maheu-Giroux and de Blois 2007; Belzile *et al.* 2010). Roads create favorable conditions for the establishment of exotic *P. australis*' colonies as they provide open spaces, free of vegetation, with good light availability (Maheu-Giroux and de Blois 2007; Brisson *et al.* 2008). Moreover, as exotic *P. australis* shows a high tolerance to salt (Mal and Narine 2004; Sun *et al.* 2007) and heavy metals (Mal and Narine 2004), it can colonize the harsh environment that roadsides provide (Lelong *et al.* 2007; Maheu-Giroux and de Blois 2007). Native *P. australis*' populations have been poorly studied in the last decade, so little information is available on their tolerance to environmental stressors. However, Sun *et al.* (2007) showed that exotic *P. australis* was more tolerant to high salt concentrations than was its native counterpart. Since roadsides receive considerable

inputs in de-icing salt, this might explain the difference in haplotype distribution in relation to the main roads.

Lelong *et al.* 2009 have identified roads as one of the key predictors of exotic *P. australis*' distribution in Quebec and Jodoin *et al.* (2008) emphasized the role of the development of the road network in the progression of the exotic *P. australis* in the 1970s. As the exotic *P. australis* is probably at the first stages of its invasion in the study area, it is likely that roads are pathways for dispersal from already occupied territory to yet unoccupied parts of the reserve. The role of roads in dispersing exotic species is well documented (e.g., Tyser and Worley 1992; Parendes and Jones 2000; Christen and Matlock 2006). The association of the exotic haplotype with roads reflects not only its tolerance to environmental stressors, but its stage of invasion in the territory.

Another distinction about the exotic and native *P. australis*' distribution was their relation to natural bodies of water. Our results indicated that native *P. australis* was more frequent than exotic *P. australis* at shorter distances to natural bodies of water. Our results are consistent with observations of Meadow and Saltonstall (2007) which found that colonies of native *P. australis* were mostly present near rivers and creeks, whereas exotic *P. australis* was mostly found in high marshes. No study has compared yet their tolerance to water level, flood frequency, or wave action. Nevertheless, the progression of exotic reed is slowed by high water levels or repeated inundation (Haslam 1972; Hudon *et al.* 2005). 49 water level measurements taken in the study area in 2000 by Environment Canada (M. Jean, unpublished) and in 2009 by S. Taddeo confirmed that water levels were higher on the shore of Lake St-François and along natural rivers than what was measured elsewhere in the study area. This could thus denote a difference in tolerance to high water level between exotic and native *P. australis*. On the other hand, propagule pressure may also be reduced nearby natural bodies of water as they are generally far from roads.

The frequency of exotic *P. australis* was high in anthropogenic land uses such as built-up areas and fallow lands. The presence of farms near wetlands has been

identified as a source of nutrients (Bertness *et al.* 2002). With nutrient enrichment, exotic *P. australis* produces more shoots, more rhizomes, more biomass, and forms denser colonies, which in turn increases its ability to shade competitors (Bertness *et al.* 2002; Minchinton and Bertness 2003; Ravit *et al.* 2007; Kettenring and Whigham 2009). Accordingly, the presence of nearby crops has been positively correlated with *P. australis*' density in American studies (Trebitz and Taylor 2007; Chambers *et al.* 2008). Fertilizer use on farmland can increase the input of nutrients in adjacent wetlands, favoring very competitive plant species that usually form monotypic stands and therefore leave fewer spaces for other species (Houlahan *et al.* 2006). A recent study showed that to be an effective competitor, exotic *P. australis* had a greater need for nutrients than native *P. australis* which was shown to be a low-nutrient specialist (Modzer and Zieman 2010), which could explain the predominance of the exotic *P. australis* in these land uses.

In agreement with the findings on native *P. australis* and natural bodies of water, native reed occurred more frequently than exotic *P. australis* in low marshes, where water levels are high, whereas only exotic *P. australis* was significantly associated with drier sites such as high marsh or swamps. The exception was shrub swamps dominated by *Alnus incana* subsp. *rugosa* which is also the most dominant land cover in the area. These swamps are marshes that are being gradually invaded by woody species, likely in response to changes in anthropogenic fire regime (Auclair *et al.* 1976; Jean and Bouchard 1993). Not surprisingly, none of the haplotypes was frequent in forest patches where access to sunlight is limited.

The “distance to dyke and canals” variable was not retained as a pertinent one to distinguish haplotypes in part because different types of dykes or canal were pooled in the analysis. The main dyke sampled tends to be invaded by the exotic *P. australis*, whereas man-made canals within the protected area tend to be associated with the native type as they are also close to natural bodies of water. Several agricultural ditches linking the St-François NWA with surrounding cropland potentially act as important

source of nutrients and may increase connectivity with surrounding land uses, which would allow for more propagules to penetrate into the protected territory. Rivers were identified as good vectors for propagule dispersal through floods (Engstrom *et al.* 2009) or rhizome transported through floating material (Minchinton 2006), but for the moment, they are still bordered by native *P. australis*.

Conclusion

Currently, the St-François NWA still serves as a refuge for the native reed which is found at higher frequency there than the exotic type. The presence of the exotic *P. australis* in this area is likely more recent than that of the native one. At this stage of invasion, the study showed that native and exotic *P. australis* still occupied distinct parts of the territory, the native one being associated more with low marsh and areas of lesser human impacts, the exotic one being closer to roads or associated with drier land covers. There are of course land covers in which both haplotypes can occur, but there are still relatively very few areas of spatial overlap between native and exotic colonies. As the exotic *P. australis* seems tolerant to a broader range of environmental conditions compared to the native one, this suggests that disturbances to a given land cover or near it may be more important in creating invasion foci than the nature of the land cover itself. Given the potential for more spatial overlap and competitive interactions with time, it will be important to monitor the future progression of both the exotic and native haplotypes to prevent large scale invasion.

Figures and tables

Figure 3.1 Study area: The Lake St-François National Wildlife Area

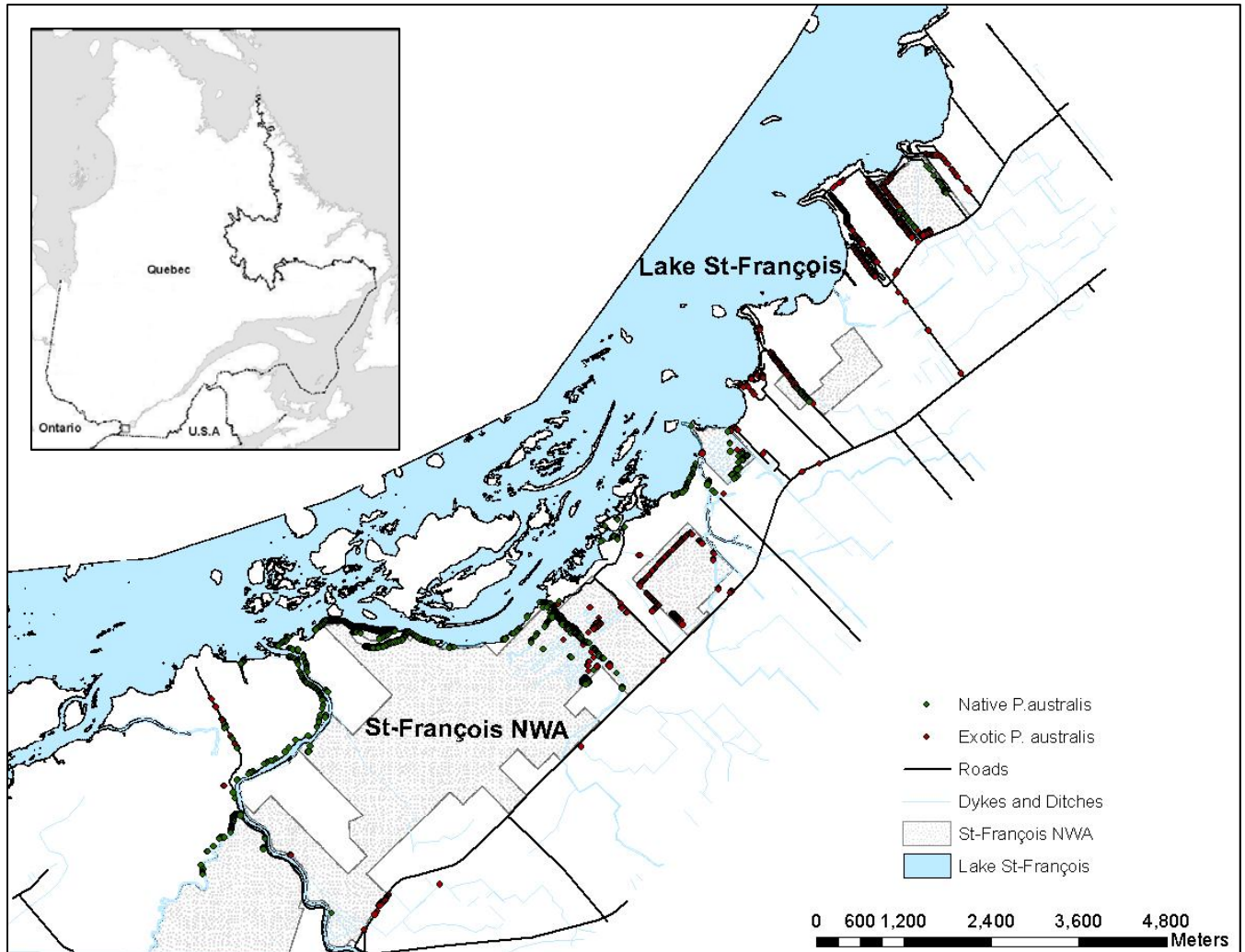


Table 3.1 Land uses and land covers used in the study and their characteristics. Adapted from Létourneau and Jean (2006).

Land uses/Land cover	Characteristics
Built up area	Includes roads, buildings, and parking.
Denuded Substrate	Less than 25% vegetation cover.
Dry meadow	Land dominated by herbaceous plants, always unwatered and not used for agriculture.
Fallow land; Fallow land dominated by <i>Populus balsamifera</i> ; Fallow land dominated by <i>Crataegus spp.</i> ; Fallow land dominated by <i>Populus tremuloides</i> ; Fallow land dominated by <i>Rhus typhina</i>	Description of this category not provided by Létourneau and Jean
Farms	Includes all crops, pasture and fodder.
Forest dominated by <i>Ulmus sp.</i>	Forests where <i>Ulmus sp.</i> covers more than 25% of the parcels.
Forested swamp; Forested swamp dominated by <i>Salix fragile</i> ; Forested swamp dominated by <i>Fraxinus pennsylvanica</i> ; Forested swamp dominated by <i>Acer rubrum</i>	Swamp with a cover of arborescent species greater than 25%.
High marsh; High marsh dominated by <i>Lythrum salicaria</i> ; High marsh dominated by <i>Carex spp.</i>	Unwatered wetland where herbaceous species are out of water during minimum flow episodes.
Low marshes; Low marsh dominated by <i>Sparganium eurycarpum</i> ; Low marsh dominated by <i>Typha spp.</i> ; Low marsh dominated by <i>Pontederia cordata</i> ; Low marsh dominated by <i>Bolboschoenus fluviatilis</i> ; Low marsh dominated by <i>Zizania spp.</i>	Wetlands periodically flooded, with a substrate continually saturated or covered by water during the growing season.
Meadow dominated by <i>Solidago spp.</i>	Dominated by herbaceous plants, always unwatered and not use for agriculture.

Table 3.1 *continued*

Land uses/Land cover	Characteristics
Open water	Bodies of water free of floating or submerging vegetation.
Ploughed land	Separated from the farms category to avoid possible conflict with the built-up area class due to their similar spectral signature.
Shrub swamp; Shrub swamp dominated by <i>Alnus incana</i> subsp. <i>rugosa</i> ; Shrub swamp dominated by <i>Salix</i> sp.	Swamp with a shrub cover greater than 25%.

Table 3.2 Scores of variables on canonical axis I. Only the variables that were selected in the forward selection of explanatory variables are displayed.

Explanatory variables	Axis I
Species	
Native <i>P. australis</i>	-3.3040
Exotic <i>P. australis</i>	3.3960
Land uses/land covers	
Low marsh dominated by <i>Zizania</i> spp.	0.1248
High marsh	0.2408
High marsh dominated by <i>Carex</i> spp.	0.0199
Forested swamp	0.0912
Farms	0.2429
Dry meadow	0.1178
Ploughed land	0.2036
Fallow land dominated by <i>Rhus typhina</i>	0.1349
Fallow land dominated by <i>Crataegus</i> spp.	0.1166
Built-up area	0.4569
Landscape variables	
Distance to roads	-0.7538
Distance to natural bodies of water	0.7400

Table 3.3 Freeman-Tukey deviates of exotic and native *P. australis* in different land uses/land covers (LULC). Freeman-Tukey deviates significantly different from the critical chi-square value are followed by a star.

LULC	Exotic <i>P. australis</i>	Native <i>P. australis</i>
Built up area	14.1951*	-16.0770*
Denuded Substrate	-0.3619	0.3767
Dry meadow	3.5812*	-5.3719*
Fallow land	1.1849	-0.9572
Fallow land dominated by <i>Populus balsamifera</i>	-4.5017*	2.5501*
Fallow land dominated by <i>Crataegus spp.</i>	3.8362*	-3.9744*
Fallow land dominated by <i>Populus tremuloides</i>	-0.7629	0.6973
Fallow land dominated by <i>Rhus typhina</i>	4.3905*	-4.7185*
Farms	7.3566*	-11.9825*
Forest dominated by <i>Ulmus sp.</i>	-1.4295	1.0642
Forested swamp	2.9970*	-3.1557*
Forested swamp dominated by <i>Salix fragilis</i>	-1.3500	0.8246
Forested swamp dominated by <i>Fraxinus pennsylvanica</i>	2.2055	-3.5688*
Forested swamp dominated by <i>Acer rubrum</i>	0.5586	-0.3865
High marsh	7.8688*	-7.9763*
High marsh dominated by <i>Lythrum salicaria</i>	1.2768	-1.0306
High marsh dominated by <i>Carex spp.</i>	0.5312	-0.4011
Low marsh dominated by <i>Sparganium eurycarpum</i>	1.5454	-1.2670
Low marsh dominated by <i>Typha spp.</i>	-15.0980*	8.8089*
Low marsh dominated by <i>Pontederia cordata</i>	-6.4643*	3.7639*
Low marsh dominated by <i>Bolboschoenus fluviatilis</i>	-11.0930*	5.7186*
Low marsh dominated by <i>Zizania spp.</i>	-4.2834*	-3.9359
Meadow dominated by <i>Solidago spp.</i>	-5.0450*	2.9985*
Open water	-7.7250*	4.8808*
Ploughed land	6.4133*	-10.1350*
Shrub swamp	-0.0176	0.1009
Shrub swamp dominated by <i>Alnus incana</i> subsp. <i>rugosa</i>	-9.3764*	6.1582*
Shrub swamp dominated by <i>Salix sp.</i>	-1.1696	0.9102
Suspended matter	-0.5860	0.5476

Table 3.4 Freeman-Tukey deviates of exotic and native *P. australis* relative to distances to roads and natural bodies of water. Freeman-Tukey deviates significantly different from the critical chi-square value are followed by a star.

Distance to road			Distance to natural bodies of water		
Distances (m)	Native	Exotic	Distances (m)	Native	Exotic
50	-16.5138*	17.7778*	50	18.4044*	-38.0399*
100	-0.2894	0.4951	100	-4.0419*	4.5673*
150	1.5161*	-3.4720*	150	-11.8344*	10.5989*
200	2.1867*	-5.4746*	200	-9.1834*	8.4179*
250	3.3516*	-8.9456*	250	-3.4668*	3.9437*
300	2.7856*	-7.2599*	300	-5.6413*	5.5252*
350	1.8255*	-3.5920*	350	-7.0079*	6.2939*
400	-0.0223	0.199	400	0.4023	-0.4857
450	1.8595*	-4.4980*	450	0.9166*	-1.2182*
500	1.9035*	-4.6294*	500	-2.8779*	3.2748*
550	-1.2082*	1.4951*	550	-8.1774*	6.4197*
600	1.8958*	-3.0985*	600	-8.2218*	6.5728*
650	0.6136*	-0.7598*	650	-7.1722*	6.4254*
700	3.9439*	-9.5949*	700	-4.4357*	4.3759*
750	4.2076*	-10.3615*	750	-2.6016*	2.7998*
800	1.7030*	-2.8334*	800	-2.9909*	3.0935*
850	0.2624	-0.1984	850	-5.3741*	4.3690*
900	0.5647	-0.6461*	900	-6.1983*	3.5606*
950	-0.8811*	0.8453*	950	-8.4830*	4.6999*
1000	1.4026*	-3.1323*	1000	-5.8362*	3.3798*
1050	3.8992*	-10.5754*	1050	-15.5952*	8.2390*
1100	3.9623*	-10.7632*	1100	-5.6478*	3.2857*
1150	4.3598*	-11.9461*	1150	-3.3342*	2.1253*
1200	4.4164*	-12.1144*	1200	-0.8817	0.846
1250	7.0199*	-19.8577*	1250	-2.3411*	1.6213*
1300	9.0753*	-25.9690*	1300	-0.8817	0.846
1350	5.0293*	-13.9378*	1350	-0.8817	0.846
1400	4.6889*	-12.9251*	1400	-2.3411*	1.6213*
1450	1.2608*	-1.9009*	1450	-2.3411*	1.6213*
1500	1.6217*	-3.7876*			

Connecting text

In the previous chapter, it was shown that the two haplotypes of *P. australis* had distinct distribution in relation to land uses/land covers and landscape variables, and the

role of disturbances in creating invasion foci for the exotic haplotype of *P. australis* was emphasized. In light of these findings, habitat suitability models and expansion models were used in Chapter 4 to map current suitable conditions for each haplotype and predict potential expansion patterns of *P. australis* in the study area.

Chapter IV

Spatially explicit tools to assess invasion risks by common reed (*Phragmites australis*) in a protected freshwater wetland*

Sophie Taddeo and Sylvie de Blois

Abstract

Controlling invasive species can be both costly and time consuming and may pose a threat to native plant species. Several authors state that prevention is the most cost-effective way to manage invasive species, but managers tend to prefer late control over prevention for lack of critical quantification of invasion risk. The objective of this study was to develop spatially explicit tools to help predict, in a protected wetland of southern Quebec, the potential current and future distributions of an invasive haplotype of *Phragmites australis* as well as of a co-occurring native haplotype. A model based on a maximum entropy approach was used to map the location of suitable conditions for each haplotype based on current environment/species relations. This information was then used in an expansion model based on clonal growth to predict their potential future expansion patterns. The results suggested that the exotic *P. australis* had the potential to expand into a larger portion of the territory than the *P. australis*, even if the native *P. australis* was currently more frequent. This was a consequence of the tolerance to a larger range of suitable conditions for the exotic *P. australis* and of the spatial configuration of current suitable patches and invasion foci. These predictions could be used to help managers of protected areas assess better the risks and consequences associated with *P. australis* in natural wetlands.

*Manuscript to be submitted to Landscape Ecology

Introduction

Introduction of exotic species are now occurring at an unprecedented rate, helped by a globalization of exchanges (Ricciardi 2007). If episodes of introduction are more frequent, potential impacts of these introductions are also exacerbated by an increased vulnerability of habitats to invasion due to anthropogenic modifications. When invading natural habitats, invasive species may have several negative impacts, as they compete with native species for space and resources, sometimes modify habitats, and potentially introduce new diseases (D'Antonio and Meyerson 2002).

Controlling invasive species can be both costly and time consuming and may pose a threat to local plant species, especially when chemical control is applied (Blossey 1999). Thus, several authors state that prevention is often the most cost-effective way to manage invasive species (e.g., Rejmanek 1999; Thuiller *et al.* 2005). Moreover, eradication and control are easier and more likely to be successful when population are small and isolated (Moody and Mack 1988; Inglis *et al.* 2006). Early intervention would also be less costly and less harmful to local species and habitats (Brown *et al.* 2008). In spite of this, Finnoff *et al.* (2007) observed that managers tend to apply control when the species is well established, because the outcome is more easily quantifiable. To be able to allocate limited resources to control invasive species efficiently, it has been suggested that managers of protected areas need relevant information about the current and potential impacts of species invasion (Byers *et al.* 2002; Foxcroft *et al.* 2007). Throughout the different steps of risk assessment, managers can evaluate risks and potential impacts posed by specific species to a territory and decide whether or not the cost of inaction are more important than cost of control. Once the potential impacts are known, vulnerability of a target site to invasion may be assessed through the utilization of habitat suitability models to identify potential foci of invasion (Byers *et al.* 2002). Information about sources of propagules and pathways of introduction may then be included to provide insights about the likelihood and amplitude of an invasion (Herborg *et al.* 2007). Moreover, spatially explicit information about the potential

spatial extent of an invasion is crucial as impacts on native ecosystems will tend to increase with spatial extent.

The overall goal of this study was to develop spatially explicit tools to help managers of protected areas estimate the risks associated with the progression of invasive species. The target species was *Phragmites australis* (Cav.) Trin. ex Steud. (hereafter referred to as *P. australis*) and the study focused on a protected wetland bordering the St. Lawrence River in southern Quebec. The specific objectives were to: 1) map potential suitable habitats for the exotic haplotype and a native haplotype of *P. australis*, and 2) model their potential expansion patterns in the study area within the next 20 years. The exotic haplotype of *P. australis* has been recognized as one of the most aggressive invaders of North American wetlands. Genetic analysis of *P. australis* populations in North America confirmed the existence of several haplotypes of common reed: an exotic invasive haplotype (haplotype M) and 11 native haplotypes (Saltonstall 2002). The exotic haplotype was probably introduced in Quebec during the late 19th century (Lelong *et al.* 2007). It remained scarce and confined to the shores of the St. Lawrence River until disturbances to wetlands, low water levels in the St. Lawrence Seaway, and the development of the roads network in the 1960s allowed its rapid progression in southern Quebec (Lelong *et al.* 2007). Nowadays, the exotic haplotype is largely dominant in Quebec (Jodoin *et al.* 2008). Its distribution is associated with roadsides (Jodoin *et al.* 2008) and linear wetlands (Maheu-Giroux and de Blois 2007), but it has also recently started to colonize natural wetlands (Lavoie 2008). Its progression in natural habitats seems to trigger a decrease in diversity and biomass of native plant species (Chambers *et al.* 1999; Warren *et al.* 2001; McGlynn 2009), a loss of habitat quality and diversity (Chambers *et al.* 1999; Weinstein and Balleto 1999), and possible negative impacts on fauna (Benoit and Askins 1999; Chambers *et al.* 1999). Inferences based on herbarium data suggest that the progression of *P. australis* could have caused a decline in the populations of native haplotypes in marshes of the United States. Recent laboratory and field evidence showed that the two haplotypes can successfully hybridize, which could lead to a more aggressive hybrid and cause genetic

pollution of the native strain (Meyerson 2007; Meyerson *et al.* 2010; Paul *et al.* 2010). As there are few colonies of native *P. australis* remaining in Quebec, and that the exotic *P. australis* has already established large monocultural communities in some marshes of the province (e.g., Boucherville Islands), there is a crucial need to assess risks of invasion in yet un-invaded or little invaded marshes to guide management decisions.

Methods

Study site

The study area is located at the Lake St-François National Wildlife Area (hereafter referred to as St-François NWA; 45° 01' N , 74° 30' W), a federally protected reserve since 1978 located on the south shore of Lake St-François at the border between the state of New York, USA and the province of Quebec, Canada (Figure 3.1). Lake St-François, located between Cornwall, Ontario (45° 01' N , 74° 45' W) and Salaberry-de-Valleyfield, Quebec (45° 15' N , 74° 08' W), is a natural widening of the St. Lawrence River. The St-François NWA comprises 1347 hectares (Ministère du développement durable de l'environnement et des parcs du Québec 2009).

In 1987, St-François NWA was conferred RAMSAR status as an internationally remarkable wetland and one of the last large remaining expanses of freshwater wetlands in the agriculturally dominated area of southern Quebec. It is situated within the hardwood forest subzone, in the sugar maple bitternut domain and is surrounded by agricultural land with corn fields or wet meadows and some low density housing (Maheu-Giroux *et al.* 2006). Climate is cool temperate with average annual temperature of 6.5 °C and average annual precipitation of 944.8 mm (Environment Canada 2009). The St-François NWA comprises several community types, including swamps dominated by shrubs such as *Alnus incana* subsp. *rugosa* (considered invasive), low marsh dominated by *Carex spp.*, *Sparganium eurycarpum*, and *Typha spp.*, high marsh dominated by *Carex spp.*, forest patches and aquatic communities (Létourneau and Jean 2006).

Although protected, the ecosystems of the St-François NWA, as most wetlands around the world, have been under increased pressures from human activities. First, the modification of the hydrological regime of Lake St-François between 1940 and 1970 for various purposes has resulted in an overall increase in mean water level and a relative stabilization of annual variation in water level compared to previous conditions (Auclair *et al.* 1973). Second, human-made fires appear to have been occurring in the St-François NWA up to the 1970s, as evidenced by field observations and the analysis of aerial photographs (Jean and Bouchard 1993; Maheu-Giroux *et al.* 2006). With the cessation of fire, large areas of the St-François NWA previously covered with *Carex spp.* dominated marsh have been invaded by *Alnus incana* subsp. *rugosa* (Jean and Bouchard 1991). Third, agricultural activities around the St-François NWA have greatly intensified in the last four decades following changes in agricultural policies and the construction of a vast network of agricultural drainage ditches to drain the rich clay soil of the region (Domon and Bouchard 2007). At some locations and because of the slope patterns, agricultural land is being drained into watercourses flowing through the St-François NWA. Fourth, Ducks Unlimited Canada in the 1980s created a network of canals to manage waterfowl use within the St-François NWA. Finally, roads and trails make some parts of the St-François NWA more accessible than others, introducing disturbances. All these changes have undoubtedly affected vegetation patterns and may have increased vulnerability to invasive species, but this has received little investigation.

Status of P. australis in the NWA

The St-François NWA is one of the few locations in Quebec that host populations of both native and exotic *P. australis* and as such may be one of the few natural refuges for the native type. It is unclear what the historical distributions of the native and exotic *P. australis* were in the St-François NWA, as the discovery of an exotic haplotype is fairly recent (Saltonstall 2002). In a study of vegetation communities, Auclair *et al.* (1973) observed that, when present, *P. australis* was dominant in emergent communities (99.9% of dry material), but only accounted for 10.9% of dry material of meadow communities. Auclair *et al.* (1976) observed a maximum biomass production of *P.*

australis in plots where water levels were around 1m. Based on current knowledge of the spatial distribution of *P. australis* in the St-François NWA, it would appear that the native haplotype is the most likely to have been sampled in their studies. Moreover, in a study of vegetation patterns along riverine systems of the same area, Jean and Bouchard (1993) reported 96 plant species from sampling done in 1986-1987, but surprisingly there was no mention of *P. australis* (complete list of species not included in their paper). A vegetation survey conducted in 2000 by Environment Canada (Létourneau and Jean 2006) mainly to validate the mapping of vegetation classes gathered from satellite imagery included 2 out of 37 quadrats with *P. australis* present. Our current observations in the field suggest that these were probably exotic *P. australis*.

Data collection and mapping

The locations of all colonies (n = 181) of *P. australis* in the St-François NWA were identified during summer and winter of two sampling seasons (2006-2007) and their boundaries recorded using a GPS receiver mobile mapper. The haplotype was identified in the field through morphological differences (red stems, narrow leaves, small inflorescence for the native *P. australis*; green stems, wider leaves and larger inflorescence for the exotic *P. australis*). DNA analysis was performed by Annie St-Louis at the Phytologie Department of Laval University in 2006 on 65 random leaf samples (37 native and 28 exotic) following the methodology of Saltonstall (2002) to validate field identification. There was 100% agreement with the field classification.

The spatial coordinates of the colonies were imported as an ArcView shapefile onto a base map of the St-François NWA, using the Universal Transverse Projection of Mercator, zone 18. The base map included different features such as roads, bodies of water, canals, dykes, and land uses/land covers (LULC) present in the study site. These features were identified through field surveys, aerial photographs, and thematic maps. National road, Lake St-François, rivers, and human-made canals were mapped by

screen-digitizing aerial photographs. The positions of secondary roads and dykes were obtained in the field, using the 'create a line' function of GPS receiver mobile mapper.

A grid of 25m² cells was created to cover the whole study area for analysis. The "polygon in polygon analysis" function of Hawth's tool 3.27, implemented in ArcGIS 9.3 was used to estimate the % cover of *P. australis* in each cell. *P. australis* was considered present when it covered at least 25% of a 25m² cell. In total, there were 6069 cells with cover records (2234 for exotic *P. australis* and 3835 for native *P. australis*, two of which had also the exotic one). All cells with or without *P. australis* were included in the models.

Four environmental variables were obtained from the base map and used to perform the analyses. These explanatory variables were: 1) distance to the nearest road (0 – 1500 m), which includes a national road as well as some secondary roads, 2) distance to natural bodies of water (0 m – 1450 m), which includes Lake St-François and three natural rivers, 3) distance to dyke and canals (0 m – 2200 m), which includes human-made canals used to drain adjacent farms or canals for waterfowl habitat, and 4) land use and land cover (LULC). The LULC classification was based on a map by Létourneau and Jean (2006) of wetlands located on the shore of Lake St-François using images taken by the remote sensing satellite Ikonos between July, 25 and August, 21 2002, with a scale of 1:50 000 and a precision of around 15 to 25 meters (see table 3.1 for a description of the categories of LULC). The Zonal Statistic ++ tool of Hawth's toolbox implemented in ArcGIS 9.3 was used to determine categories of land use or land cover in cells. The Euclidean distance function of the Spatial Analyst Tool implemented in ArcGIS 9.3 was used to measure the Euclidean distance from the centroid of a cell to a given feature.

Analyses

Four models were constructed: 1) an habitat suitability model for the exotic *P. australis*; 2) an expansion model for the exotic *P. australis* with a time horizon of 20 years; 3) an habitat suitability model for the native *P. australis*; 2) an expansion model

for the native *P. australis* with a time horizon of 20 years. The habitat suitability models were done to map the location of suitable conditions for each haplotype based on current environment/species relations. The expansion models served to predict the potential future expansion patterns of each haplotype based exclusively on clonal growth and consequently identify potential zones of overlap and competition. Since they are based only on clonal growth and ignore the contribution of seed dispersal, the expansion models are considered conservative.

Maheu-Giroux and de Blois (2007) showed a high level of spatial autocorrelation among exotic *P. australis*' patches along linear wetland habitats. Data is considered as autocorrelated when the value at a given point is not independent from values at neighboring points, which may violate the assumption of independence of data required by several statistical analyses (Dormann *et al.* 2007). Ignoring this problem might also inflate model's performance (Dormann *et al.* 2007; Parolo *et al.* 2008). In preliminary analyses, a Moran's I correlogram, which is constructed by computing a measure of similarity between pairs of points as a function of their distances from each other, was built using cover data of the exotic reed to assess the maximal distance at which two points of occurrence were autocorrelated. Similarity measures were then compared to an expected value in absence of autocorrelation using the following formula;

$$E(I) = -1/(n - 1)$$

where $E(I)$ is the expected value in absence of autocorrelation for the site I and n is the sample size (Dormann *et al.* 2007). The statistical significance of the Moran's I coefficient was then tested with the Moran's I standard deviate test (Dormann *et al.* 2007). This analysis showed that cover data were autocorrelated up to a distance of 8.5 meters. Thus, only points that were separated by at least 9 meters were used in all predictive models.

Habitat suitability models

MaxEnt 3.3.1, a software that uses an algorithm based on a maximum entropy approach, was used to map the potential distribution of each haplotype. MaxEnt uses only presence data. The use of presence only model was favored as the actual distribution of the exotic *P. australis*, which is at an early stage of invasion in the St-François NWA, does not necessarily reflect all the conditions that are unsuitable for the species. This type of model was proven to have prediction capacities similar to models using presence-absence data (Elith *et al.* 2006). MaxEnt seeks to create a distribution of probabilities based on presence and background data, with the constraints that the distribution is the closest to uniformity and that it matches the empirical average of environmental variables (Philips *et al.* 2004). Once the distribution of probabilities is known, the spatial distribution of predictors is used to compute a probability of presence from 0 (low chances) to 1 (high chances) in each cell of the study site. MaxEnt has been widely used in recent years to predict potential distribution of non-indigenous species (e.g., Gibson *et al.* 2007; De Meyer *et al.* 2010) and rare species (e.g., De Marco *et al.* 2008; Parolo *et al.* 2008) for which data on true absences may be lacking. This algorithm generally performs very well (Evangelista *et al.* 2008) and often better than other modelling methods (e.g., GARP, GAM, GLM and BIOCLIM) (Gibson *et al.* 2007; Evangelista *et al.* 2008), but it tends to be conservative (Peterson *et al.* 2007).

Pearson (2007) suggested splitting data into a test set and a training set when an independent set of data is not available to test model accuracy. Following this approach, for each habitat suitability model, 70% of occurrence points were randomly selected to construct the models and 30% of the remaining points were used to validate it. For native *P. australis*, 1,008 occurrence data and 11,008 background points were used to create the habitat suitability model, and 288 occurrence points were used to test it using 100 iterations. As there are fewer colonies of exotic *P. australis* currently found in the area, 674 points of occurrence and 10,674 background points were used to construct the models, and 288 to test them. An Area Under the Receiver Operating Characteristic Curve (AUC), in which sensitivity (i.e. number of presences or absences

correctly predicted) is computed as a function of specificity (i.e. number of presences or absences incorrectly predicted) using different thresholds, was then used to assess the accuracy of the models (Pearson 2007). A jackknife distribution of explanatory variables was constructed by running models using one explanatory variable at a time, and by running models excluding one variable at a time, to assess the contribution of each explanatory variable to the overall AUC of models.

Expansion models

Expansion models based on observed clonal growth rates in St-François NWA were created to predict the potential future expansion patterns over the next 20 years of each haplotype based exclusively on clonal growth and consequently identify potential zones of overlap and competition between the haplotypes. The model is constructed as a cellular automaton; from a given cell with an invaded state, the species will spread in neighboring cells (using Moore neighborhood) that have been defined as suitable in the habitat suitability models (i.e. where the probability of presence is superior to 0.5) (Figure 4.1). The cell can therefore have a “partially invaded” state. As cells have dimensions of 4 m by 4 m and a speed of spread of 2 m per years is used, it takes two years for a cell to reach a “completely invaded” state. The average annual speed of spread is based on recent field measurements of *P. australis*’ progression, both exotic and native, in St-François NWA (Denis *et al.*, unpublished data) and is consistent with other measurements in southern Quebec (e.g., Hudon *et al.* 2005; Lavoie 2007). An alternative scenario was also used to model the expansion of exotic *P. australis*. In this scenario, the exotic haplotype could spread everywhere, but in cells occupied by forests or open bodies of water. As exotic *P. australis* is currently at the beginning of its invasion, its potential suitable habitats are probably underestimated. Thus, the use of two scenarios, one with constraints and the other without constraints, may be more realistic. Scenarios were implemented in Matlab 2010b.

Results

Habitat suitability models

The overall performances of habitat suitability models for the exotic and native *P. australis* were very good. The models for the exotic *P. australis* had an average AUC of 0.995, and a standard deviation of 0.002 between the different runs. The average AUC of the native models was lower at 0.987, with a standard deviation of 0.001.

For the exotic *P. australis*, the distance to roads was the variable with the most weight in the models (62%), followed by distance to natural bodies of water (22.7%), distance to dyke and ditches (13.4%), and LULC (1.9%). Distance to roads was not only the best variable to predict the occurrence of exotic *P. australis*, but it was also providing the greatest amount of information that was not already contained in other variables as indicated by its AUC score when ran separately (Figure 4.2). LULC have a substantial contribution to the regularized training gain, whereas the variables distance to natural water and distance to dykes and ditches have lower predictive capacities. The suitable conditions in which the exotic *P. australis* could potentially be found covered a total area of 6 km² (Figure 4.3). Exotic *P. australis* was mainly distributed near secondary roads and the highway.

The distance to dyke and ditches and distance to natural bodies of water were the variables with the strongest weight in the native model (respectively 49% and 43.6%), whereas LULC (5.1%) and distances to roads (2.3%) had a smaller contribution. Accordingly, the jackknife distribution of explanatory variables showed that the distance to road variable did not improve much the model, as its removal does not affect the total AUC (Figure 4.2). When the contribution of each variable is tested independently of the others, LULC is the variable that has the strongest predictive capacity. Distance to natural water and distance to dykes and ditches are the variables that have the greatest effect on the regularized training gain when removed, implying that they provide novel information that is not contained in other explanatory variables. The suitable conditions in which the native *P. australis* could potentially be found covered a total area of 4.53

km² (Figure 4.4). Suitable habitats were located mainly close to natural bodies of water and on the shore of Lake St-François.

Expansion models

Although native *P. australis* currently occupies more cells than its introduced counterpart, expansion models predicted that within 10 years, the exotic *P. australis* could surpass native *P. australis* in terms of cover (Figures 4.5). Expected cover for the exotic *P. australis* in 2030 could range from 0.7 km² (scenario with constraints) to 0.8 km² (scenario without constraints), whereas native *P. australis* is expected to cover 0.5 km² (Figure 4.5). Within 20 years, our expansion models predicted that exotic *P. australis* could be covering 13% of the total area identified as potentially suitable for it. This translates to a potential increase of 894% (scenario without constraints) to 936% (scenario with constraints) of its present cover.

A potential first zone of contact between exotic and native *P. australis* appeared in the expansion models around 2020, at less than 20 m from a ditch (Figure 4.6). In 2030, five zones of contact were visible; four of these being located within a distance of 30 m from a ditch, and the fifth one located 15 m away from a secondary road (Figure 4.7).

Discussion

The importance of roads and anthropogenic disturbances for the exotic *P. australis* is confirmed by this study. As stated earlier, St-François NWA experienced many changes in the past century. Among them, an intensification of agriculture (Maheu-Giroux *et al.* 2006), and a control of water level (Jean and Bouchard 1991) greatly affected the composition of plant communities. These modifications may also have facilitated the progression of exotic *P. australis* by providing more nutrients and limiting water level fluctuations. As roads are a major pathway of introduction of propagules in the area, management efforts could be targeted towards minimizing the impacts of the roads already in place by restoring their roadsides or monitoring their surroundings.

The considerable weight given to the distance to natural bodies of water variable should also be taken into account. As explained in Chapter 3, few colonies of exotic *P. australis* are currently found near natural bodies of water where water levels are probably deeper. Consequently, probabilities of presence of exotic *P. australis* are lower when located at small distances from Lake St-François or one of the three natural rivers. Priority may thus be given to restoring or protecting communities located further away from bodies of water, where the likelihood of an invasion is greater.

According to the models, St-François NWA and its surroundings contain at least 6 km² of habitats in which conditions are favorable to the establishment of exotic *P. australis*. However, it should be kept in mind that the potential future distribution of *P. australis* in this area is very likely underestimated, as only current conditions of establishment are projected. Thus, the expansion model is conservative and may not be capturing certain conditions under which *P. australis* can survive and which are not represented in its current distribution. Moreover, the model only accounts for clonal expansion. Recent studies showed that seedling establishment is possible in Quebec (Brisson *et al.* 2008), and is probably the strategy used by the species to colonize new open environments (Belzile *et al.* 2010), especially after disturbances. Seedling establishment is reported to be successful on bare soils located close to bodies of water (Mal and Narine 2004). New colonies of exotic *P. australis* could thus establish near sites with denuded substrate or in locations such as ditches where disturbances may leave bare soil.

Adding a component of propagule pressure allowed getting a better sense of the capacities of the species to spread across the patches that are designated as suitable for it. As such, the model of clonal expansion predicted that within 20 years, exotic *P. australis* could be covering 13% of the territory identified as suitable for it, which represents an increase of 894% (scenario with constraints) to 936% (scenario without constraints) of its actual cover. The majority of this increase is taking place in the

protected portion of our study area, with the exception of a few colonies located close to a natural river in a territory that is mainly not inhabited.

Among the five different parcels that constitute the St-François NWA, two are completely covered by potential habitats for exotic *P. australis* and three are partially covered (Figure 4.3). However, the major portion of the St-François NWA that remains free of predicted invasion foci is already covered by shrubs swamps dominated by *Alnus incana* subsp. *rugosa*, a native shrub considered invasive and usually associated with a low diversity. On the contrary, protected portions where many invasion foci are predicted to occur are characterized by a higher diversity of habitats; they include several LULC such as high marshes dominated by *Carex spp.*, dry meadows, low marshes dominated by *Zizania spp.* and low marshes dominated by *Typha spp.*

The drastic predicted increase in exotic *P. australis* could have important impacts on the native one. Even if the distribution of potential habitats was initially larger for the native sub-species, the clonal expansion model predicted that the exotic sub-species would have a larger total coverage than the native one within 10 years. This was the consequence of the different spatial configuration of the distribution of potential habitats for both sub-species. The distribution of potential habitats for the exotic *P. australis* is constituted of three main blocks, all of these currently containing colonies of exotic *P. australis*. On the contrary, potential habitats for the native *P. australis* are much more scattered and fragmented; patches are smaller and isolated, and several are located far from patches where native *P. australis* is currently occurring. This implies that the native reed could have more difficulty dispersing into these potential habitats from its current location, at least using clonal expansion. These distribution patterns might be the consequence of a broader tolerance to environmental conditions by the exotic *P. australis*, as it is able to persist in both disturbed anthropogenic land uses, where the native *P. australis* is almost absent, as well as in more natural land covers. Moreover, these predictions reflect different realities at the population level. Denis *et al.* (unpublished data) observed similar speed of progression for the exotic and native *P.*

australis, but significant differences in their rate of densification. Exotic *P. australis* colonies are generally producing more stems per year. These observations are consistent with those of League *et al.* (2006) who showed that exotic *P. australis* generally grew faster and produced more biomass and more stems than the native one in similar conditions.

Our results suggest that even when using a conservative expansion scenario, the exotic *P. australis* has the capacity to cover a significant portion of St-François NWA. This drastic increase may result in increasing difficulties in controlling the exotic *P. australis* and raise control costs. Control of invasive species is more efficient when populations are small and isolated (Inglis *et al.* 2006), as propagule pressure increases with time and the number of invasion foci. If the ecological impacts inherent to the establishment of exotic *P. australis* in freshwater wetlands have been little studied so far, several studies showed considerable issues in brackish and saltwater wetlands, where colonies were associated with a decrease in quality and diversity of habitats and a low faunal utilization (Weinstein and Balleto 1999).

Conclusion

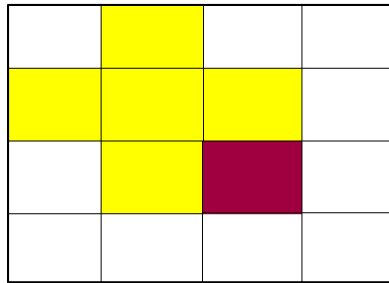
Using predictive models that combined propagule pressure, invasibility of sites estimated from habitat suitability models, and time, the potential future expansion patterns of the exotic and native haplotypes of *P. australis* in a protected wetland of southern Quebec were estimated for the next 20 years. Using conservative expansion parameters, the results suggested that the exotic *P. australis* had the potential to expand into a larger portion of the territory than the native *P. australis*, even if the native *P. australis* currently occupies more cells. This is a consequence of the tolerance to a larger range of suitable conditions for the exotic *P. australis* and of the spatial configuration of current suitable patches which are widely distributed for the exotic *P. australis* with invasion foci already present, whereas the suitable habitat for the native *P. australis* are more scattered and still unoccupied.

As there has been little study of the ecology of *P. australis* in freshwater wetlands, consequences of this progression on biodiversity are hard to evaluate. There is no doubt however, that *P. australis* has the capacity to greatly impact the conservation value of this protected area. Managers should aim to protect plant communities, especially those sheltering species at risk, located in the parts most vulnerable to invasion as identified by this study. Sites where an overlap between exotic and native *P. australis*' distributions is possible should also be carefully monitored, as the outcome of competition between these two haplotypes is still little understood, and as recent research showed that they could produce viable hybrids.

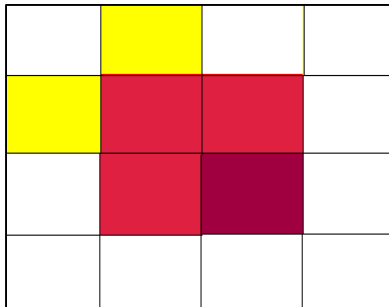
Figures

Figure 4. 1 Functioning of the expansion model

Time step 1: One cell is completely invaded; six were defined as suitable through the habitat suitability models.



Time step 2: *P. australis* has progressed into the three suitable cells adjacent to the already occupied one. These three cells are attributed a partially invaded stage.



Time step 3: The cells that were partially invaded at time 2 are now completely invaded.

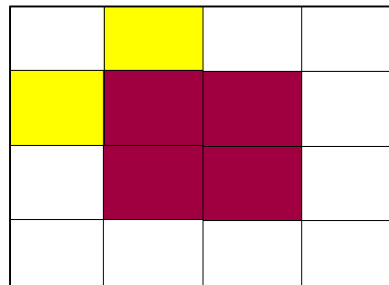
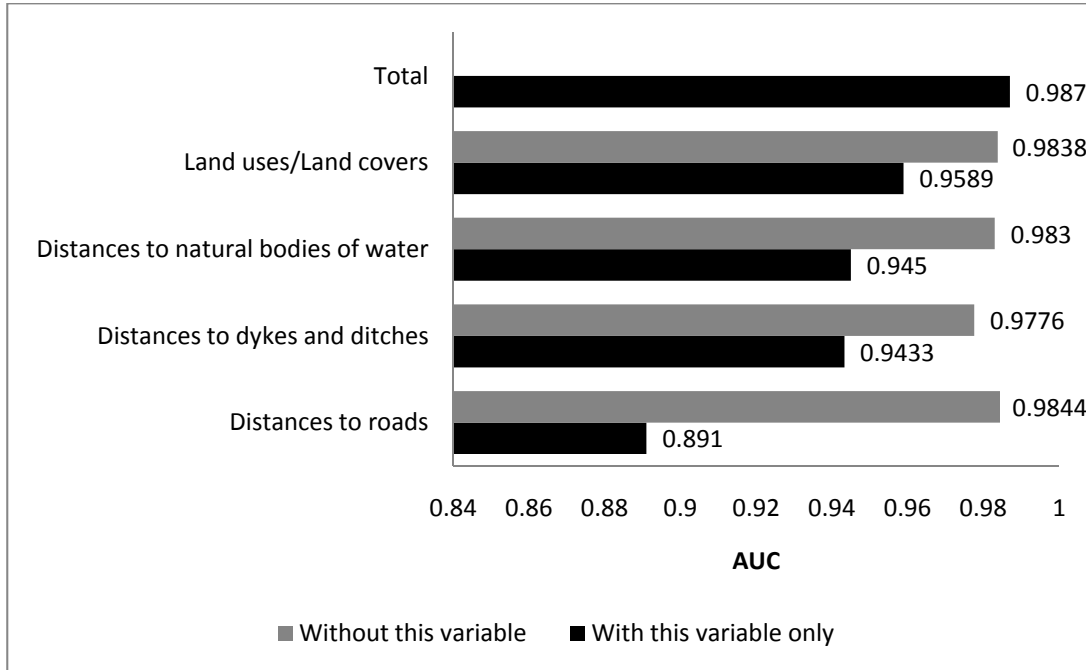


Figure 4. 2 Contribution of explanatory variables to the performance of the native *P. australis* and exotic *P. australis'* models as measured by the Area under receiver operator curve (AUC).

Native *P. australis* model



Exotic *P. australis* model

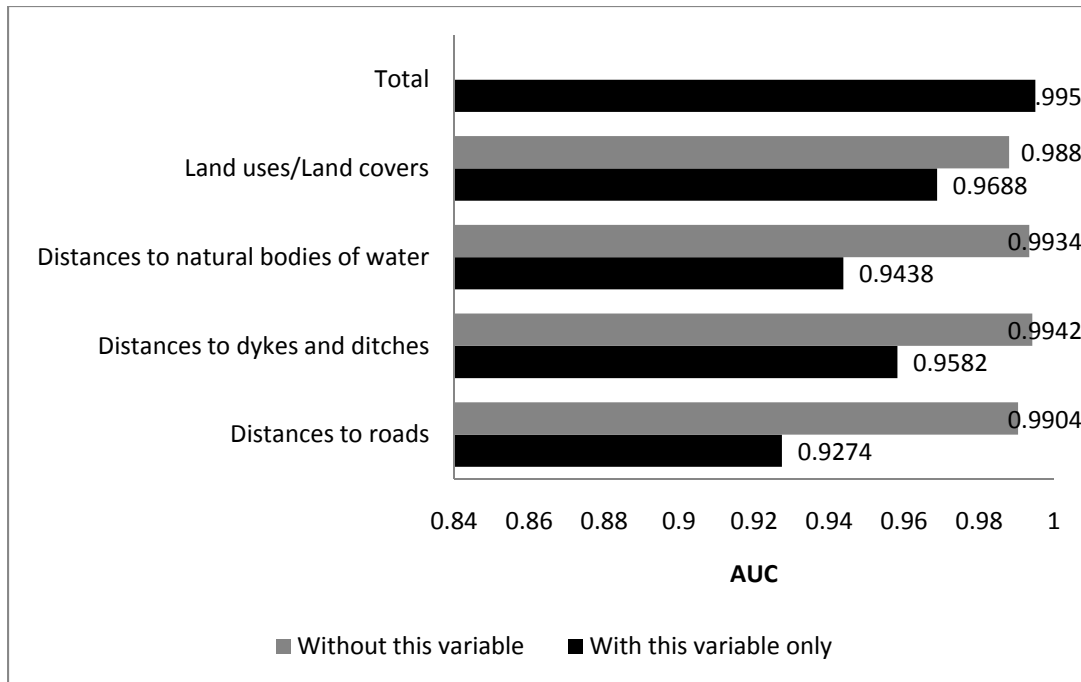


Figure 4. 3 Map showing current observed distribution and the probability of presence (suitable habitat) predicted by MaxEnt for exotic *P. australis* in the St. François NWA and adjacent areas.

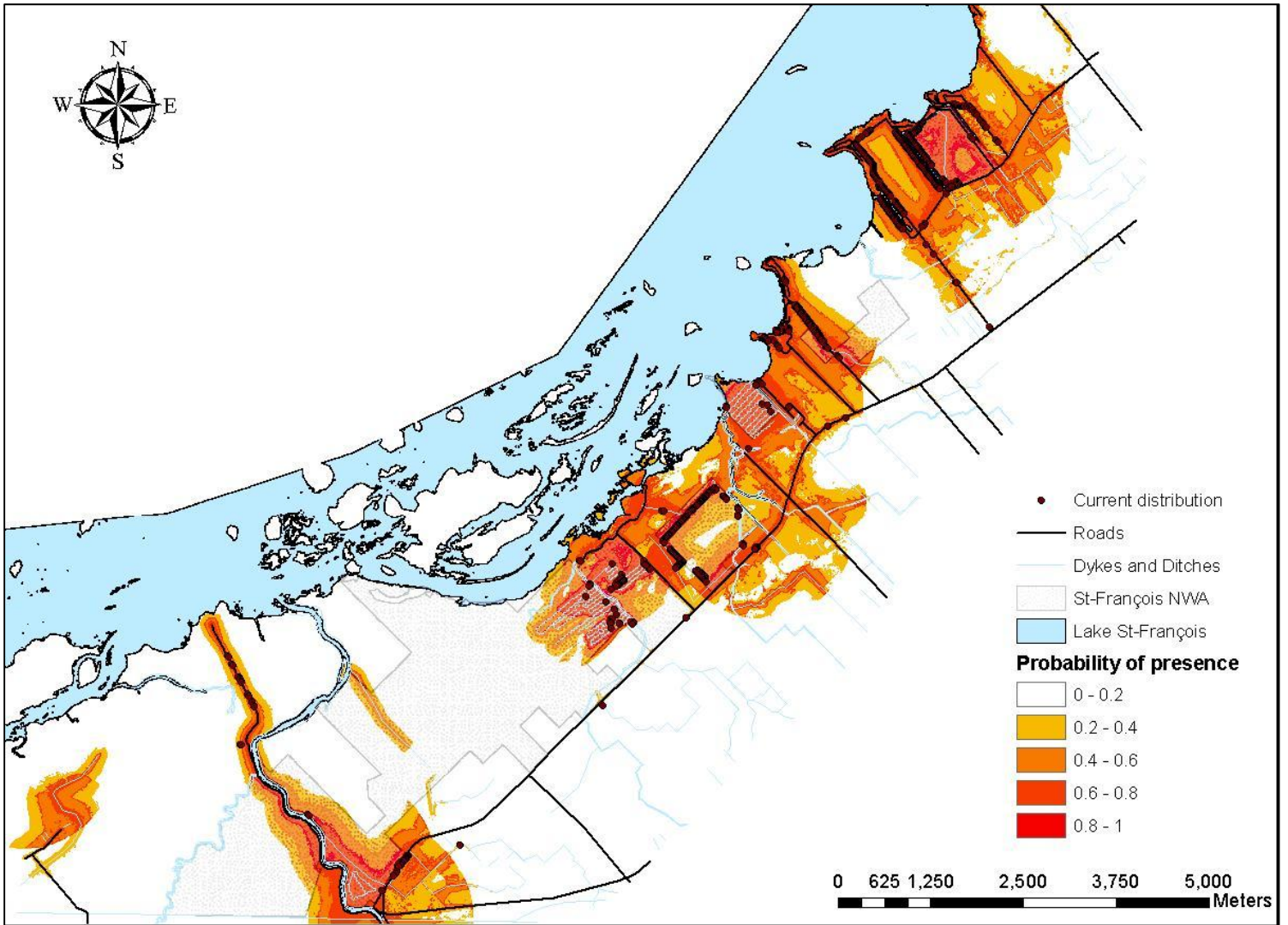


Figure 4. 4 Map showing current observed distribution and the probability of presence (suitable habitat) predicted by MaxEnt for native *P. australis* in the St. François NWA and adjacent areas.

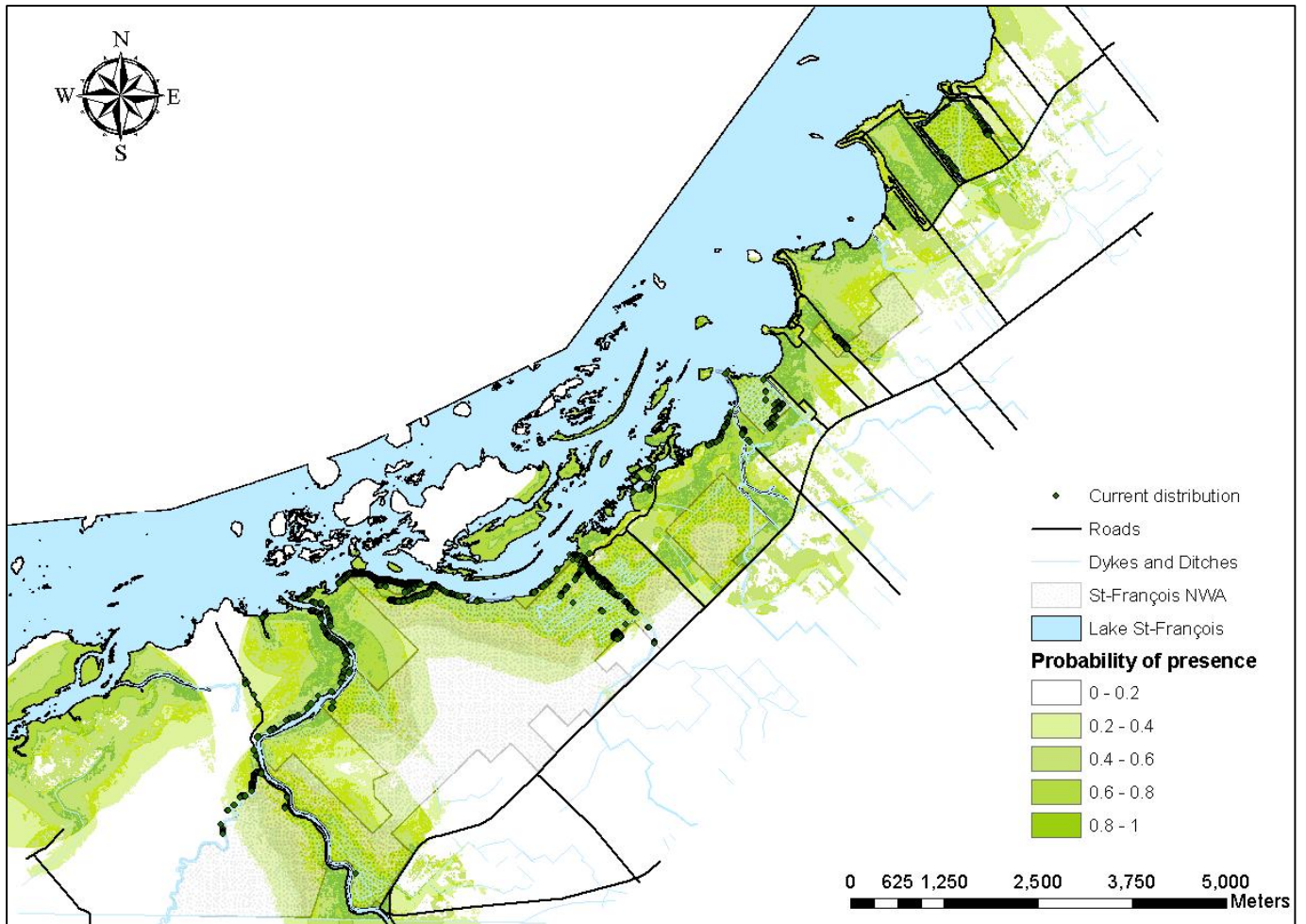


Figure 4. 5 Predictions of expansion models based on clonal growth showing the total potential area covered by exotic *P. australis* (in red) and native *P. australis* (in green) with time. For exotic *P. australis*, the dark red line indicates a scenario with constraints (i.e., the species can establish only in suitable cells) and the light red indicates a scenario without constraints (i.e., all adjacent cells are available for establishment).

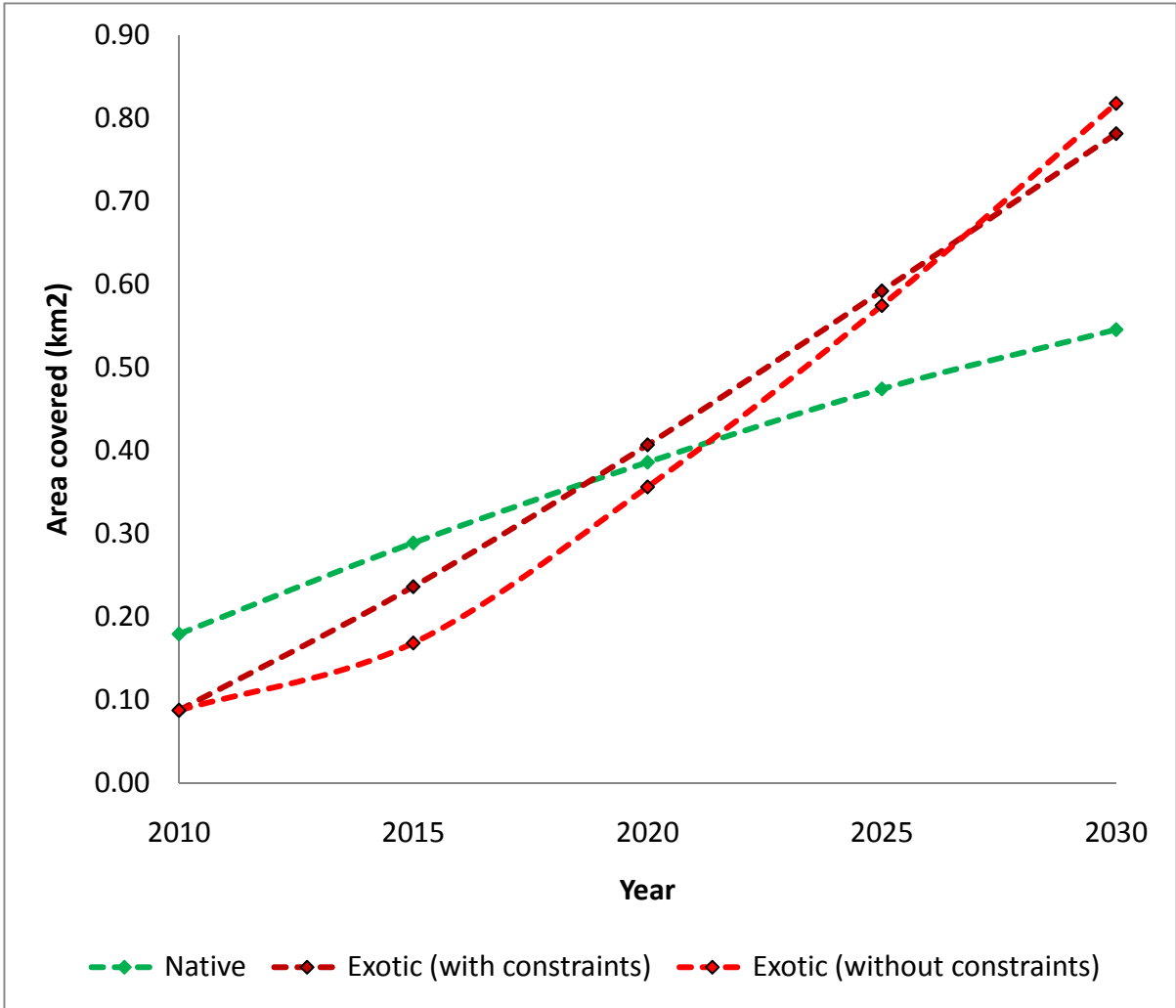








Figure 4.6 Predicted potential distribution of colonies of exotic *P. australis* (in red) and native *P. australis* (in green) in 2020, according to a scenario of clonal growth without constraints for the exotic *P. australis* only (above) and with constraints (below).



Legend

-  Ditches
-  Roads
-  NWR St-François
-  Lake St-François

Native reed occurrence

-  Partially covered
-  Completely covered

Exotic reed occurrence

-  Partially covered
-  Completely covered

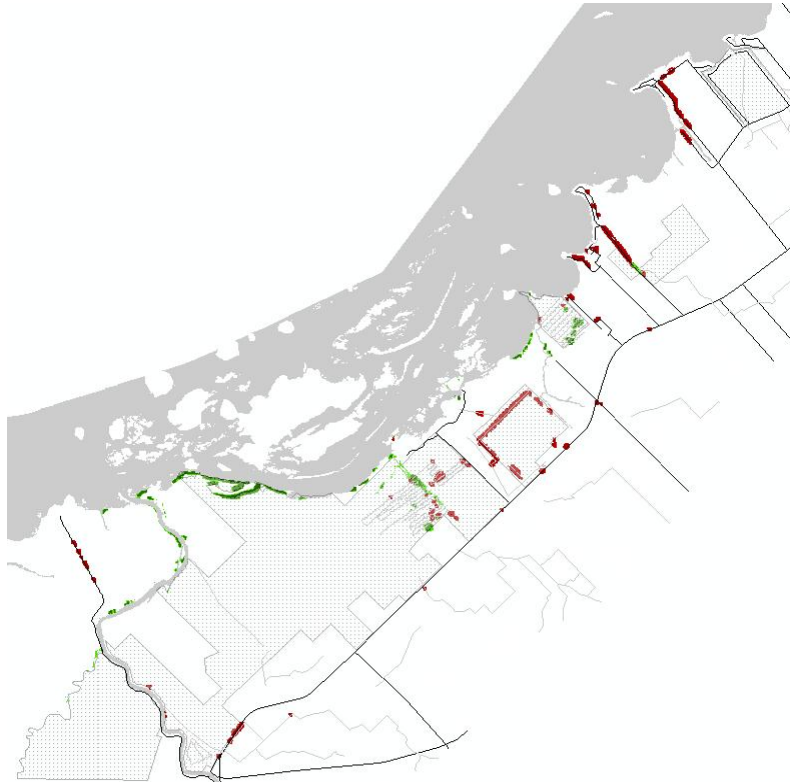
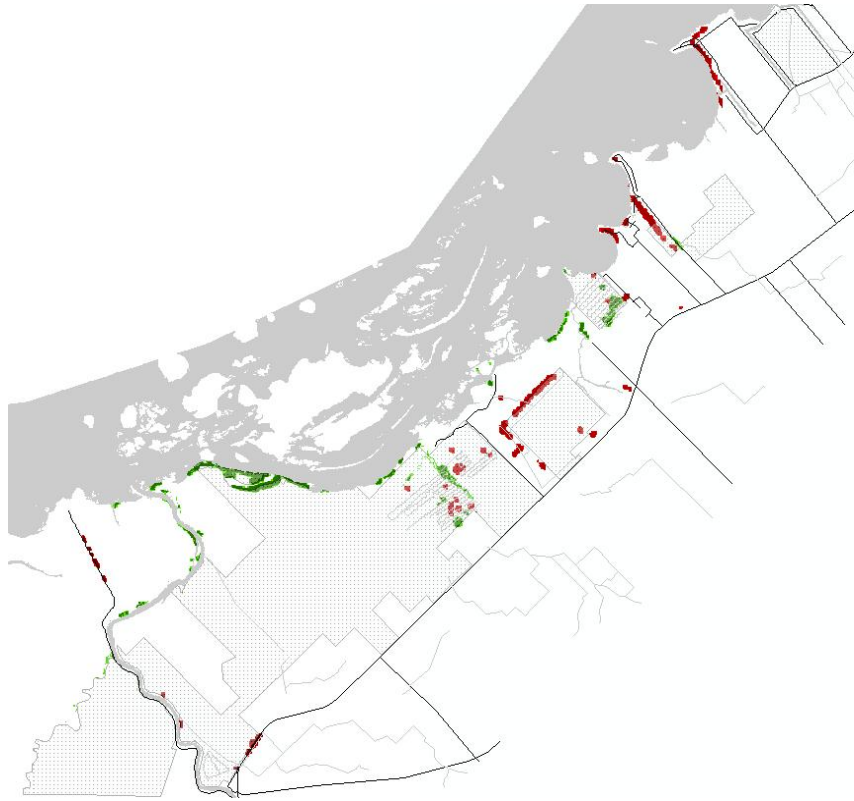
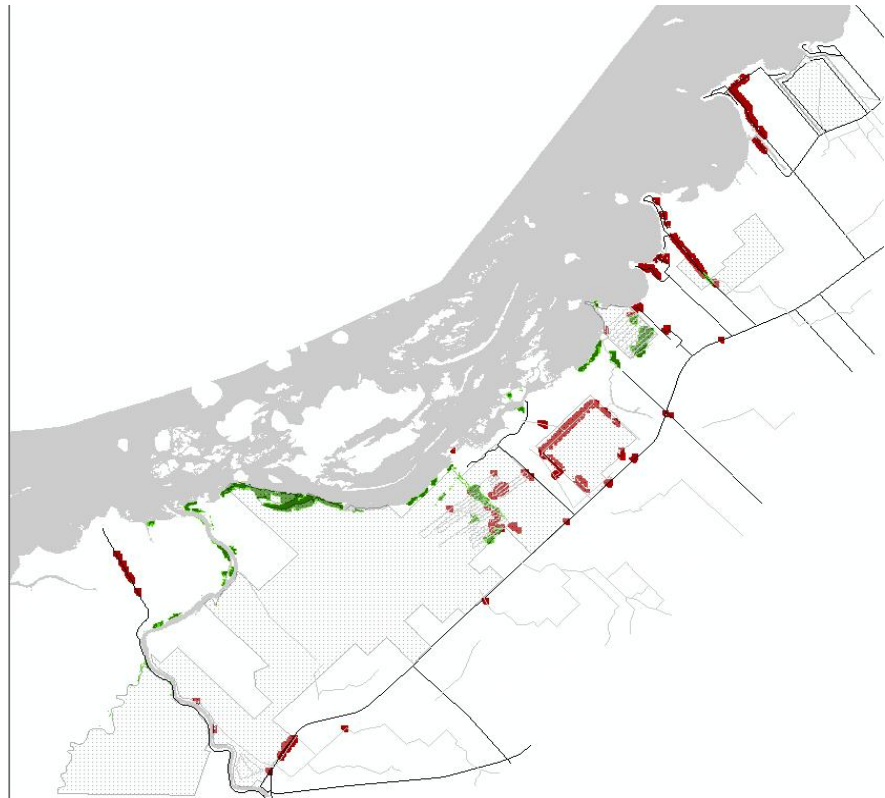


Figure 4.7 Predicted potential distribution of colonies of exotic *P. australis* (in red) and native *P. australis* (in green) in 2030, according to a scenario of clonal growth without constraints for the exotic *P. australis* only (above) and with constraints (below).



Chapter V. General conclusion

Findings presented in chapter III showed that the exotic *P. australis* could be associated with a broader range of conditions than its native counterpart. Once small-scale perturbations allow its establishment, exotic *P. australis* can colonize both anthropogenic and natural sections of the wetland. This broad range of tolerance resulted in a potential to cover a greater portion of the protected area than its native counterpart. Within 20 years, the expansion and invasion models presented in Chapter IV predicted that exotic *P. australis* could increase its current distribution by 894% based on a conservative clonal growth model. This progression could have significant impact on the conservation value of the territory, on management decisions for control, and on native colonies co-occurring in the area.

As very few colonies of native *P. australis* remain in Quebec, there is a crucial need for a long term assessment of contact zones to assess if exotic *P. australis* has the capacity to displace its native counterpart at broad spatial scales. Special attention should be paid to hybridization between the haplotypes, as it could further threaten the survival of native *P. australis*.

Controlling the progression of the invasive haplotype of *P. australis* in protected wetlands might be quite challenging, especially if these wetlands are sheltering rare or endangered species. So far, most control methods tested are expensive and potentially detrimental to the local flora (e.g., herbicides and burn-herbicide treatments). Additionally, a rapid restoration of the controlled area would be required to prevent the re-establishment of colonies, adding to the cost of control. Thus, understanding conditions that allow the establishment of exotic *P. australis*' populations and preventing these conditions to occur when possible may be the best way to curb the progression of the exotic *P. australis*. The approach developed in this thesis can provide guidance to help managers prioritize areas vulnerable to invasion and decide whether, when, and where control is warranted.

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