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Coexistence of introduced and native common reed (*Phragmites australis*) in freshwater wetlands[1]

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Abstract: Invasive species are especially problematic when introduced into ecosystems with native congeners. The extent to which niches overlap in space determines whether the introduced species threatens the native one or the native species can escape competition or the effect of control. We compared the spatial distribution in relation to landscape and land-use/land-cover variables of introduced and native *Phragmites australis* (common reed) in a landscape of protected freshwater wetlands in Quebec, Canada. Results showed that the wetlands still serve as refuges for native *P. australis*. At this stage of invasion, native and introduced *P. australis* occupy distinct spatial niches, the more abundant native type in low marsh and areas of lesser human impacts, the introduced one closer to roads and drier land covers. For now, native *P. australis* largely escapes competition, and the lack of spatial overlap could reduce opportunities for hybridization. Our study also suggests that invasion foci could still be controlled without endangering the native type. Whether the heterogeneous wetland conditions and the different spatial niches will be sufficient to allow long-term coexistence of native and introduced *P. australis* remains to be seen, but the situation needs to be closely monitored, especially in wetlands protected for biodiversity conservation.

Keywords: ecological niche, exotic invasive species, invasion pathways, protected areas, St-François National Wildlife Area, St. Lawrence wetland.

Résumé : Les espèces envahissantes peuvent être particulièrement problématiques lorsqu'elles sont introduites là où se trouvent des congénères indigènes. La répartition spatiale des niches détermine si l'espèce introduite menace l'indigène ou si l'indigène peut échapper à la compétition ou aux effets nuisibles du contrôle. Nous avons comparé la répartition spatiale en fonction de variables du paysage et de couverture et d'utilisation du sol de deux types de *Phragmites australis* (roseau commun), l'un indigène et l'autre introduit, dans des marais protégés du sud du Québec. Les résultats montrent que ces milieux humides servent toujours de refuge au roseau indigène. À ce stade-ci de l'invasion, les deux roseaux occupent encore des niches spatiales distinctes, le roseau indigène, plus abondant, étant lié aux bas marais et aux milieux peu perturbés, le roseau introduit se trouvant près des routes et dans les milieux plus secs. Pour l'instant, le roseau indigène échappe à la compétition et le peu d'interactions spatiales entre l'indigène et l'introduit pourrait contribuer à réduire les opportunités d'hybridation. Notre étude suggère aussi qu'il est encore possible de contrôler les foyers d'invasion sans nuire au roseau indigène. La coexistence à long terme des deux roseaux reste à déterminer, mais la situation doit être suivie de près surtout pour des milieux humides voués à la conservation de la biodiversité.

Mots-clés : aires protégées, espèce exotique envahissante, milieux humides du St-Laurent, niche écologique, Réserve nationale de faune du Lac Saint-François, voies d'invasion.

Nomenclature: Brouillet *et al.*, online.

Introduction

When entering protected areas, invasive species can act in synergy with other stressors to affect native species and their habitat, sometimes resulting in extirpations (D'Antonio & Meyerson, 2002; Gurevitch & Padilla, 2004; Ricciardi, 2004). The control of an invasive species may be particularly challenging where a phylogenetically related native species co-occurs. If the congeners share common ecological requirements, there is a greater chance that they will compete for space and resources (Thum & Lennon, 2010). The species with a superior capacity to function with limited resources or to access resources, or the one that has been released from herbivores and parasites, will often become dominant (Keane & Crawley, 2002; Mitchell & Power, 2003; Vermeulen *et al.*, 2009; Modzer & Zieman, 2010). Furthermore, if a native and introduced species were to hybridize, as sometimes happens for plants, invasion potential could be enhanced (Ellstrand & Schienrenbeck, 2000; Zalapa, Brunet & Guries, 2010). Studying the extent to which the niches of 2 closely related species—one native, one introduced—overlap in space may help determine whether the introduced species poses an immediate threat to the native one or the native species can escape competition (Byers *et al.*, 2002). Such information is also useful when management of the invasive species, especially through herbicides, can threaten the native one.

We used the cosmopolitan common reed (*Phragmites australis*), a tall macrophyte of wetlands, as a model species to explore the ecological and management issues raised by the co-occurrence of native and introduced congeners or conspecifics. An invasive Eurasian haplotype (haplotype M, *sensu* Saltonstall, 2002) of *P. australis* was likely

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introduced into North America at the beginning of the 19th century and rapidly invaded coastal wetlands (Marks, Lapin & Randall, 1994; Saltonstall, 2002; Minchinton & Bertness, 2003; McCormick *et al.*, 2010a). In Quebec, it underwent rapid spread during the 1970s, favoured by the expansion of the road network, low water levels in the St. Lawrence Seaway, and the disturbance of natural wetlands (Brisson, de Blois & Lavoie, 2010). The introduced *P. australis* is now widely distributed along the major roads and highways of southern Quebec and other linear wetlands (Maheu-Giroux & de Blois, 2005; 2007; Jodoin *et al.*, 2008) and has started to invade freshwater wetlands (Lavoie *et al.*, 2003; Hudon, Gagnon & Jean, 2005; Leblanc, de Blois & Lavoie, 2010). The latter type of ecosystem is where the introduced reed is more likely to interact with a native subspecies, *P. australis* subsp. *americanus*, but it is unclear whether they share the same spatial niche.

Herbarium data suggest that the introduced *P. australis* may be displacing populations of the native one in marshes of the United States (Lambert & Casagrande, 2006) and eastern Canada (Lelong *et al.*, 2007), although direct information about interactions is lacking. Recent laboratory and field evidence has shown that the introduced and native *P. australis* can hybridize. This could lead to a more aggressive hybrid and swamping of the gene pool of the native strain (Meyerson, 2007; Meyerson, Viola & Brown, 2010; Paul *et al.*, 2010), but genetic analysis of remaining stands of the subsp. *americanus* along the Atlantic coast suggests that this has yet to happen (Saltonstall, 2011). As the similarities and differences between these haplotypes have been mostly studied at the physiological or population level (*e.g.*, Vasquez *et al.*, 2005; League *et al.*, 2006; Packett & Chambers, 2006; Modzer & Zieman, 2010) or the broad regional scale (Lambert & Casagrande, 2006; Meadows & Saltonstall, 2007; Jodoin *et al.*, 2008), there is a need for studies that enhance our comprehension of their ecology at the landscape scale where they co-exist. Here, we focused on a large federally protected wetland reserve of the St. Lawrence River system in southern Quebec, Canada, to compare the distribution of the introduced and the native type in order to gain insight into their spatial patterns of coexistence and improve our understanding of the invasion dynamics and management of the introduced species.

Methods

Our 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 established in 1978 and situated 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 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 Lake St-François NWA comprises 1347 ha divided into 5 sections (Ministère du Développement durable, de l'Environnement et des Parcs du Québec, 2009). In 1987, it was given RAMSAR status as an internationally recognized wetland and one of the last large remaining expanses of freshwater wetlands in the agricultural south of Quebec. The St-François NWA is situated within the northern temperate zone and the sugar maple/bitternut hickory vegetation domain of Quebec and is surrounded by agricultural land with cornfields or wet meadows and some low-density housing (Maheu-Giroux, de Blois & Jobin, 2006). Average annual temperature is 6.5 °C and average annual precipitation is 944.8 mm (Environment Canada, online). The St-François NWA comprises several community types, including swamps dominated by shrubs such as *Alnus incana* subsp. *rugosa*, low marsh dominated by *Carex* spp., *Sparganium eurycarpum*, and *Typha* spp., high marsh dominated by *Carex* spp., forest patches, and aquatic communities (Létourneau & Jean, 2006). The construction of a network of canals to manage waterfowl and drainage ditches to drain agricultural lands likely affected vegetation patterns and may have increased vulnerability to plant invasion.

The locations of all colonies (n = 181) of *P. australis* in the St-François NWA were identified during summer and winter of 2 sampling seasons (2006 & 2007), and their boundaries were recorded using a GPS receiver mobile mapper. The winter survey was done to take advantage of frozen ground to reach distant colonies that had been identified while flying over the area. The status of the colonies (introduced or native) was identified in the field through morphological differences (colour of stem, size of leaves, and inflorescence). Blind (*i.e.*, no prior knowledge of classification) DNA analysis was performed in 2006 to validate field identification of 65 randomly chosen leaf samples (37 native and 28 introduced) following the methodology of Saltonstall (2002). There was 100% agreement between the DNA analysis and field identification.

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 Mercator Projection, zone 18. The base map included 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. A national highway, Lake St-François, rivers, and constructed 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 25-m^2 cells was created to cover the whole study area for analysis. The "polygon in polygon analysis" function of Hawth's Analysis Tools 3.27, implemented in ArcGIS (version 9.3.1, ESRI^{TM}, Redlands, California, USA) was used to estimate the percent cover of *P. australis* in each cell. *Phragmites australis* was considered present when it covered at least 25% of a 25-m^2 cell. In total, 4134 cells with cover records (2783 for introduced *P. australis* and 1351 for native *P. australis*, 2 of which also had the introduced species) were used for statistical analyses. Cells with no *P. australis* were not included as the focus was on comparing the conditions associated with each type of reed.

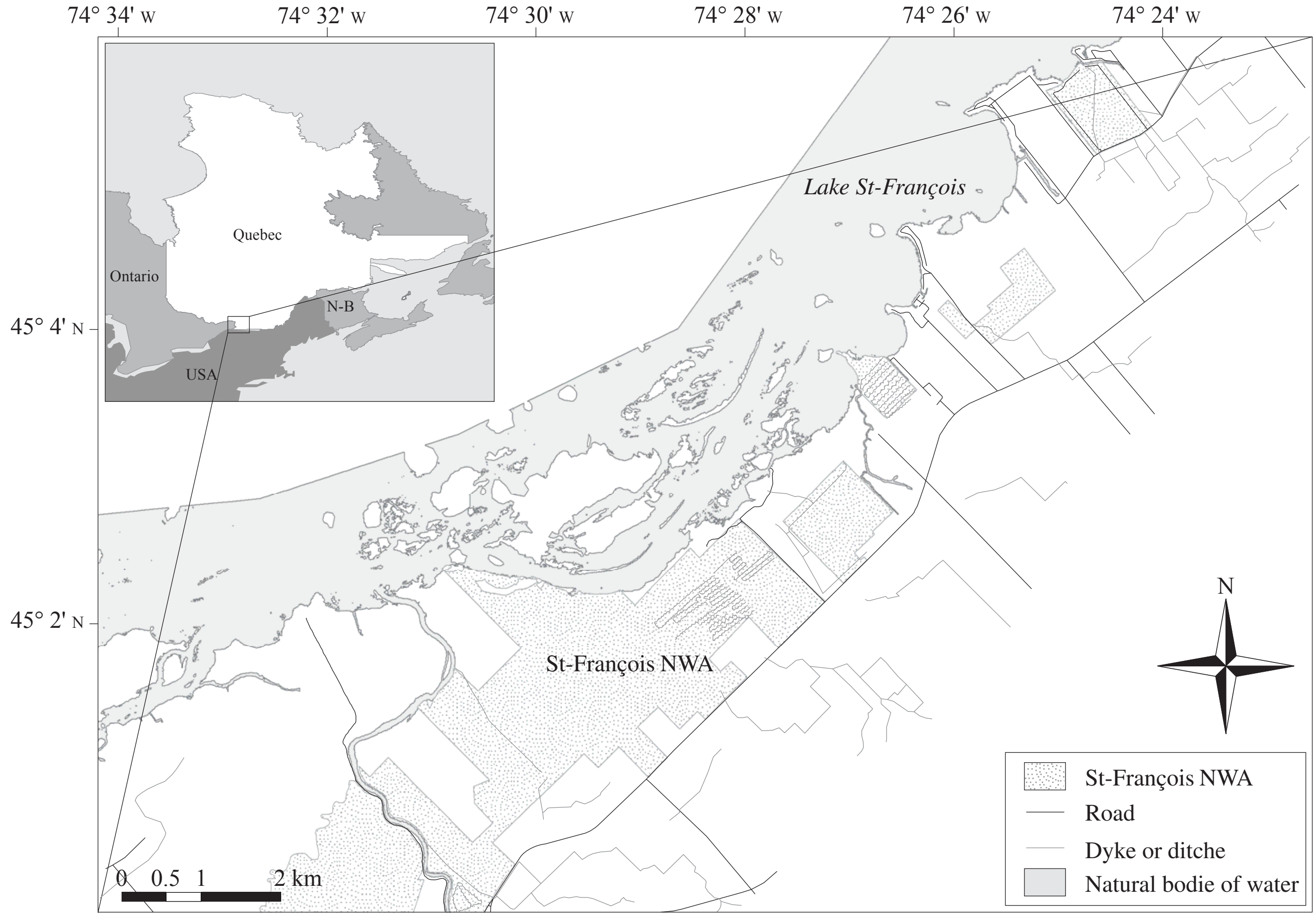

FIGURE 1. Study area: The Lake St-François National Wildlife Area.

Four explanatory variables, including landscape variables and LULC variables, were obtained from the base map and used to perform the analyses. These variables were 1) distance to the nearest road (0–1600 m), including a national highway and secondary roads; 2) distance to natural bodies of water (0–1400 m), including Lake St-François and 3 natural rivers; 3) distance to dyke and canals (0–1600 m), including constructed canals used to drain adjacent farms or for waterfowl habitat; and 4) LULC variables. The explanatory variables were chosen to capture features of the landscape that could act as invasion corridors (*e.g.*, roads, canals), indicated anthropogenic impacts (*e.g.*, fallow land, built-up areas, farms), or delineated variations in water level and associated plant cover (*e.g.*, low marsh *versus* high marsh *versus* meadow). The LULC classification was adapted from a map of Lake St-François wetlands made from IKONOS images taken between 25 July and 21 August, 2002, at a scale of 1:50 000 and precision of around 15 to 25 m (Létourneau & Jean, 2006). The Zonal Statistic ++ tool of Hawth's toolbox implemented in ArcGIS was used to determine categories of LULC in cells (more than one LULC could be considered). Some of the original LULC classes were merged to facilitate their interpretation. The Euclidean distance function of the Spatial Analyst Tool in ArcGIS was used to measure the Euclidean distance from the centroid of a cell to a given landscape feature.

Variation partitioning was conducted to identify which set of variables (*i.e.*, landscape *versus* LULC) best explained the percent cover of the native or introduced *P. australis* in cells. We used the varpart function (version 1.16-32, P. Legendre, Montréal, Canada) of the vegan library implemented in R (version 9.11, R Foundation for Statistical Computing, Vienna, Austria). Explanatory variables were standardized to facilitate their comparison, nominal variables were treated as binary variables, and a Hellinger transformation was applied to the response variables (*i.e.*, introduced or native *P. australis* cover).

A contingency table was built for each set of explanatory variables in order to determine which LULC or which distance class best accounted for the difference between cells occupied by native or introduced *P. australis*. A Pearson chi-square test was done through the function chisq.test implemented in R to test for the independence of paired observations of the response variable. Finally, a Freeman–Tukey test was conducted to test the statistical significance of the difference between observed values and expected values.

Results

In 2006, native *P. australis* covered 116 157 m^2 and introduced *P. australis* covered 79 176 m^2 of the study area. Variation partitioning showed that the combination of landscape and LULC variables explained 40% of the variation in coverage of native or introduced *P. australis*. Landscape variables (*i.e.*, distance measures) made the strongest contribution, with an adjusted R^2 of 0.35, whereas LULC had an adjusted R^2 of 0.05.

The chi-square test showed that LULC was able to distinguish sites occupied by introduced *P. australis* from sites occupied by native *P. australis* (Table I). Freeman–Tukey deviates showed that the introduced *P. australis* was more frequent than expected in all significant anthropogenic land uses, *i.e.*, built-up areas, fallow lands, and farms. Introduced *P. australis* was also significantly more frequent than the native one in high marshes and forested swamps. Native *P. australis* was more frequent than expected in low marshes and shrub swamps (Table I). The difference between the frequencies of introduced and native *P. australis* was not statistically significant in the meadows, forest, and denuded substrate classes.

The chi-square test on landscape variables showed that distances to roads, natural bodies of water, canals, and dykes were all significant in distinguishing sites occupied by introduced *P. australis* from sites occupied by native *P. australis*. Introduced *P. australis* was more frequent than expected when located less than 100 m from a road (Table II) and when located less than 100 m from a dyke or canal (Table III), whereas native *P. australis* was significantly more frequent than expected in all other significant classes of distances to road, dykes, and canals (Tables II and III). Neither sub-species was found at distances to roads greater than 1600 m. Native *P. australis* was more frequent than expected in cells located less than 100 m from a natural body of water, and introduced *P. australis* was more frequent in all other significant classes (Table IV).

Discussion

Native *P. australis* is still more abundant than introduced *P. australis* in the St-François NWA, a situation that contrasts with what has been reported for many marsh sites on the Atlantic coast (Saltonstall, 2002; Chambers *et al.*, 2008; but see also Meadows & Saltonstall, 2007) or in novel habitats (Maheu-Giroux & de Blois, 2007). The historical distribution of *P. australis* is not well established, as identification of the introduced type was fairly recent

TABLE I. Freeman-Tukey deviates of native and introduced *Phragmites australis* cover for different land uses/land covers (see Letourneau & Jean 2006 for a more detailed description of classes). Freeman-Tukey deviates higher than the critical chi-square value (χ^2 = 2.08) are indicated by an asterisk ($P < 0.01$).

LULC	Native	Introduced
Low marshes	6.5092*	–11.1286*
High marshes	–3.3542*	4.4017*
Shrub swamps	4.4503*	–7.2440*
Forested swamps	–2.1865*	2.6709*
Meadows	0.6363	–0.8631
Built-up areas	–12.8672*	12.0939*
Fallow lands	–3.6295*	4.2121*
Farms	–13.7918*	8.5801*
Forest	1.0902	–1.7051
Denuded substrate	0.6079	–0.7544

TABLE II. Freeman-Tukey deviates of native and introduced *Phragmites australis* cover for different distances to roads. Freeman-Tukey deviates higher than the critical chi-square value (χ^2 = 2.18) are indicated by an asterisk ($P < 0.01$).

Distance to roads	Native	Introduced
100	–13.833000*	15.91352*
200	1.724713	–4.45514*
300	3.192817*	–9.14703*
400	0.716634	–0.97394
500	1.724713	–4.45514*
600	0.731449	–1.02770
700	2.295826*	–4.09421*
800	3.235024*	–7.80618*
900	0.379682	–0.40928
1000	0.726302	–0.97070
1100	4.264516*	–12.56500*
1200	4.804619*	–14.28670*
1300	9.231174*	–28.38980*
1400	5.609185*	–16.85080*
1500	1.936063	–5.13203*
1600	0.953170	–1.97376

TABLE III. Freeman-Tukey deviates of native and introduced *Phragmites australis* cover for different distances to dyke and canals. Freeman-Tukey deviates higher than the critical chi-square value (χ^2 = 2.17) are followed by an asterisk ($P < 0.01$).

Distance to dyke and canals	Native	Introduced
100	–8.205820*	10.33037*
200	3.378415*	–7.41707*
300	4.277550*	–9.97616*
400	2.327544*	–4.04616*
500	2.240212*	–3.91921*
600	3.458105*	–6.86131*
700	3.583234*	–8.32837*
800	2.477272*	–4.98717*
900	1.090660	–1.68032
1000	0.417680	–0.49407
1100	1.777800	–3.29855*
1200	0.107120	–0.02884
1300	1.018900	–2.18598
1400	2.615811*	–7.30511*
1500	0.900710	–1.35096
1600	5.025359*	–12.37900*

TABLE IV. Freeman-Tukey deviates of native and introduced *Phragmites australis* cover for different distances to natural bodies of water. Freeman-Tukey deviates higher than the critical chi-square value (χ^2 = 2.22) are followed by an asterisk ($P < 0.01$).

Distance to water	Native	Introduced
100	12.33490*	–24.56030*
200	–11.44830*	11.374190*
300	–4.58167*	5.393904*
400	–2.16758	2.812488*
500	–0.36780	0.570531
600	–9.11659*	7.409160*
700	–6.48461*	6.406426*
800	–4.02420*	4.273006*
900	–7.29419*	5.424977*
1000	–8.62055*	5.005734*
1100	–13.98340*	7.811441*
1200	–1.52697	1.245102
1300	–1.52697	1.245102
1400	–1.52697	1.245102

in North America and a continuous monitoring record is lacking, but it is likely that the invasive *P. australis* was only recently introduced into the St-François NWA. In a study of vegetation communities in the same area, Auclair, Bouchard, and Pajaczkowski (1973) observed that, when present, *P. australis* was dominant in emergent communities (*i.e.*, 99.9% of dry plant material), but only accounted for 10.9% of dry material of meadow communities. Auclair, Bouchard, and Pajaczkowski (1976) observed maximum biomass production of *P. australis* in plots where water levels were around 1 m. Based on our current observations of the spatial distribution of *P. australis* in the St-François NWA, the native subspecies is the one most likely to have been sampled in their studies. On the other hand, a vegetation survey conducted in 2000 by Environment Canada in the same area (Létourneau & Jean, 2006) reported the presence of *P. australis* in 2 out of 37 quadrats. Our efforts to locate these 2 quadrats in the field indicate that they most likely contained introduced *P. australis*. This study area therefore provides a unique opportunity to understand interactions between invasive and native conspecifics and may serve as one of the last important refuges for *P. australis* subsp. *americanus* in the northern part of its range.

The distribution patterns of *P. australis* were explained first by their spatial relationship to linear features (roads, dykes, etc.) and natural bodies of water and then by their association with specific LULC. Introduced *P. australis* was more abundant than native *P. australis* near roads and was associated with anthropogenic land covers such as farms, fallow lands, and built-up areas, patterns that mimic those reported at the regional scale (Lelong *et al.*, 2007; Lelong, Lavoie & Thériault, 2009; McCormick *et al.*, 2010b). Native reeds were more abundant at short distances to natural bodies of water, where the introduced *P. australis* was scarce. These patterns support the hypothesis of recent invasion by the introduced reed through disturbances and linear corridors.

The role of roads in facilitating the dispersal of invasive species is well documented (*e.g.*, Tyser & Worley, 1992; Parendes & Jones, 2000; Christen & Matlock, 2006); these features are known to provide safe germination sites for seedlings of introduced *P. australis* (Brisson, Paradis & Bellavance, 2008). However, native *P. australis* colonies in the study area were only found close to low-traffic secondary roads that penetrated the reserve, not along the main road, in spite of the fact that the secondary roads connect to the main one. This suggests that these native colonies were already established when the secondary roads were built. The native reed seems to rely more on vegetative spread than seeds for dispersal (S. de Blois, pers. obs.), whereas the spatial patterns of invasion in linear habitats (Maheu-Giroux & de Blois, 2007), direct field observations (Brisson, Paradis & Bellavance, 2008), and genetic analyses (Belzile *et al.*, 2010; McCormick *et al.*, 2010a,b) provide strong evidence for the contribution of sexual reproduction to the dispersal and establishment of the introduced *P. australis*.

Native *P. australis* was more frequent than introduced *P. australis* at shorter distances to natural bodies of water and in low marsh, whereas introduced *P. australis* was significantly associated with drier sites such as high marsh or swamps. No study has compared their tolerance to water level, flood frequency, or wave action. Nevertheless, the progression of introduced *P. australis* is slowed by high water levels or repeated inundation (Haslam, 1972; Hudon, Gagnon & Jean, 2005), and it was found not to invade the more natural riparian areas of an otherwise highly invaded system of linear wetlands that included roadside and agricultural ditches (Maheu-Giroux & de Blois, 2007). The native subspecies *americanus* has been observed in tidal river systems on the eastern shore of Maryland (Meadows & Saltonstall, 2007). Forty-nine water level measurements taken in the study area in 2000 by Environment Canada (M. Jean, unpubl. data) and in 2009 by S. Taddeo confirmed that water levels were, as expected, higher on the shore of Lake St-François and along natural rivers than at other sites measured elsewhere in the study area. This could denote a difference in tolerance to high water levels between introduced and native *P. australis*, in particular for the establishment of seedlings of introduced *P. australis*. Unsuitable germination sites and low propagule pressure from the introduced type, as natural bodies of water are generally far from roads, could combine to limit invasion. In other systems, rivers were identified as good vectors for propagule dispersal through floods (Engstrom, Nilsson & Jansson, 2009) or rhizomes transported by floating material (Minchinton, 2006), but for now rivers are still dominated by native *P. australis* in our study area. The heterogeneous wetland conditions and possibly the different ecological niches of the introduced and the native type, resulting from different physiological tolerance, still allow coexistence in this landscape.

Built-up areas, fallow lands, and farms may act in synergy with roads to increase opportunities for invasion. Fertilizer use on farmland increases nutrient input in adjacent wetlands, favouring competitive plant species that usually form monotypic stands (Bertness, Ewanchuk & Silliman, 2002; Houlahan *et al.*, 2006). A recent study showed that to be an effective competitor, introduced *P. australis* has a greater need for nutrients than the native type, which was considered a low-nutrient specialist (Modzer & Zieman, 2010). With nutrient enrichment, the introduced *P. australis* produces more shoots, more rhizomes, and more biomass and forms denser colonies, which increases its ability to shade competitors (Bertness, Ewanchuk & Silliman, 2002; Minchinton & Bertness, 2003; Ravit *et al.*, 2007; Kettenring & Whigham, 2009). Accordingly, the presence of nearby crops has been positively correlated with *P. australis* density in American studies (Trebitz & Taylor, 2007; Chambers *et al.*, 2008). As the introduced *P. australis* seems able to colonize a broader range of environmental conditions compared to the native one, however, disturbances to a given land cover may be more important in creating invasion foci than the nature of the land cover itself.

Conclusion

Currently, the St-François NWA still serves as a refuge for native *P. australis*, which is more abundant there than the introduced type. At this stage of invasion, native and introduced *P. australis* still occupy distinct parts of the territory, the native one being associated more with low marsh and areas of lesser human impacts, the introduced one being closer to roads or associated with drier land covers. There are land covers in which both can occur, but there are still few areas of spatial overlap between native and introduced colonies. By providing information about invasion foci, our results thus demonstrate the potential to identify specific areas for control without endangering the native type. The ability to manage the invasive reed without harming the native one has been a major topic of interest in the US, especially as herbicides are widely used for control, which is not yet the case in Quebec wetlands. Given the potential for increased spatial overlap and competitive interactions with time, we also recommend modeling and monitoring the progression of both the introduced and the native *P. australis* to assess the potential for a large-scale invasion like those observed elsewhere. This is important as there seem to be few refuges left for *P. australis* subsp. *americanus* south of our study area. Our findings suggest that, for now, the native *P. australis* is able to escape competition with the introduced reed; the lack of spatial overlap may also reduce opportunities for hybridization and help to maintain distinct phenotypes. Whether heterogeneous wetland conditions and different ecological niches will be sufficient to allow long-term coexistence of the native and introduced reeds remains to be seen, but the situation needs to be closely monitored, especially in internationally significant wetlands protected for biodiversity conservation.

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