RESEARCH ARTICLE

Landscape ecology of *Phragmites australis* invasion in networks of linear wetlands

Mathieu Maheu-Giroux · Sylvie de Blois

Abstract The interaction between landscape structure and spatial patterns of plant invasion has been little addressed by ecologists despite the new insights it can provide. Because of their spatial configuration as highly connected networks, linear wetlands such as roadside or agricultural ditches, can serve as corridors facilitating invasion at the landscape scale, but species dynamics in these important habitats are not well known. We conducted a landscape scale analysis of *Phragmites australis* invasion patterns (1985–2002 and 1987–2002) in two periurban areas of southern Québec (Canada) focusing on the interaction between the network of linear wetlands and the adjacent land-uses. Results show that, at the beginning of the reference period, the two landscapes were relatively non-invaded and populations occurred mostly in roadside habitats which then served as invasion foci into other parts of the landscape. The intrinsic rates of increase of *P. australis* populations in linear anthropogenic habitats were generally higher than those reported for natural wetlands. Riparian habitats along streams and rivers were little invaded compared to anthropogenic linear wetlands, except when they intersected transportation rights-of-way. Bivariate spatial point pattern analysis of colonization events using both Euclidian and network distances generally showed spatial dependence (association) to source populations. An autologistic regression model that included landscape and edaphic variables selected transportation rights-of-way as the best predictor of *P. australis* occurrence patterns in one of the landscapes. Given the high invasion rates observed, managers of linear wetlands should carefully monitor expansion patterns especially when roads intersect landscapes of conservation or economic value.

Keywords Invasive species · Agricultural weed · Common reed · Corridor · Linear habitat · Autoregressive model · Network-*K* function · Road ecology · Spatial point pattern analysis · Autocorrelation

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Introduction

The interaction between landscape structure and spatial patterns of plant invasion has been little addressed by ecologists despite the new insights

and opportunities it can provide (With 2002). The recent and rapid expansion of *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), an emergent macrophyte showing invasive behavior in wetlands of eastern North America, provides a unique opportunity to relate invasion patterns to landscape structure. *P. australis* is considered a noxious weed at the federal and state level in the United States (US Department of Agriculture 2003). In Canada, the species is becoming a nuisance in prime agricultural land where it obstructs drainage ditches and competes with adjacent crops. In natural wetlands, it can replace native plant species (Keller 2000; Saltonstall 2002; Lavoie et al. 2003) and may affect habitat quality and possibly ecosystem functions (Weinstein and Balletto 1999; Gratton and Denno 2005). As populations continue to spread aggressively, the species is receiving increased attention for its ecological and economic effects on both natural and anthropogenic systems.

Several studies have quantified invasion patterns of *P. australis*, often in coastal wetlands, using remote sensing in order to gain insights into the processes that facilitate invasion (Weisser and Parsons 1981; Krumscheid et al. 1989; Havens et al. 1997; Kotschy et al. 2000; Rice et al. 2000; Lathrop et al. 2003; Wilcox et al. 2003; Hudon et al. 2005). However, other types of habitats often largely ignored in ecological studies (Forman and Alexander 1998) can play an important role in invasion patterns at the landscape scale. In central Canada (Québec and Ontario), evidence from field survey (Catling et al. 2003), herbarium records (Delisle et al. 2003), and remote sensing (Maheu-Giroux and de Blois 2005) show an extensive colonization by *P. australis* of linear anthropogenic wetlands such as drainage ditches along highways and agricultural lowlands. Because of their spatial configuration as highly connected networks, linear wetlands have the potential to serve as corridors that facilitate dispersal at the landscape scale and subsequent invasion into the natural or anthropogenic ecosystems that they intersect. This suggests that the effective management of *P. australis* has to take into account the interaction between natural and anthropogenic habitats, but invasion patterns in anthropogenic habitats have yet to be assessed.

In this study, we conduct a landscape-scale analysis of *P. australis* invasion patterns in two periurban areas of southern Québec, focusing on the interaction between the network of linear anthropogenic wetlands and the adjacent landscape. Specifically, we (1) provide a detailed reconstruction of invasion patterns from historical remote sensing data, (2) analyze colonization events using spatial point pattern analysis adapted to a network, and (3) test a predictive model of *P. australis* occurrence in the network of linear wetlands that incorporates landscape variables. Our study also provides a detailed methodological approach for the study of spatial patterns in linear habitat networks.

Materials and methods

Study area

The study was conducted in two periurban landscapes of southern Québec, Canada. The first landscape (1326 ha) is located on the south shore of Montréal, near Saint-Bruno-de-Montarville, hereinafter referred to as St-Bruno, (45°30′ N, 73°19′ W) and the second one (1446 ha) is at the eastern tip of Laval Island (45°39′ N, 73°36′ W), about 27 km North-West of St-Bruno (Fig. 1). These study sites met the following criteria: (1) presence of *P. australis* populations, (2) heterogeneous land-uses/land-covers, (3) complex network of linear wetlands, and (4) availability of historical large-scale aerial photographs. Genetic analyses using RFLP techniques (Saltonstall 2003) have demonstrated that *P. australis* populations of both landscapes are from the invasive European genotype, haplotype ''M'' (B. Lelong., unpublished data). One highway (Highway 30, built in 1975), a major road (route 116, built in1940 but widened to 4 lanes in 1959), and a railroad (built at the end of the 19th century) pass through St-Bruno. In Laval, a railroad (also built at the end of the 19th century), and two major roads (Avenue Marcel-Villeneuve built in 1989 and Avenue Lortie built in 1984) cross the landscape. Both landscapes also include an extensive network of drainage ditches associated with agricultural fields and other land-uses. In Québec,

Fig. 1 Localization map of the St-Bruno and Laval landscapes
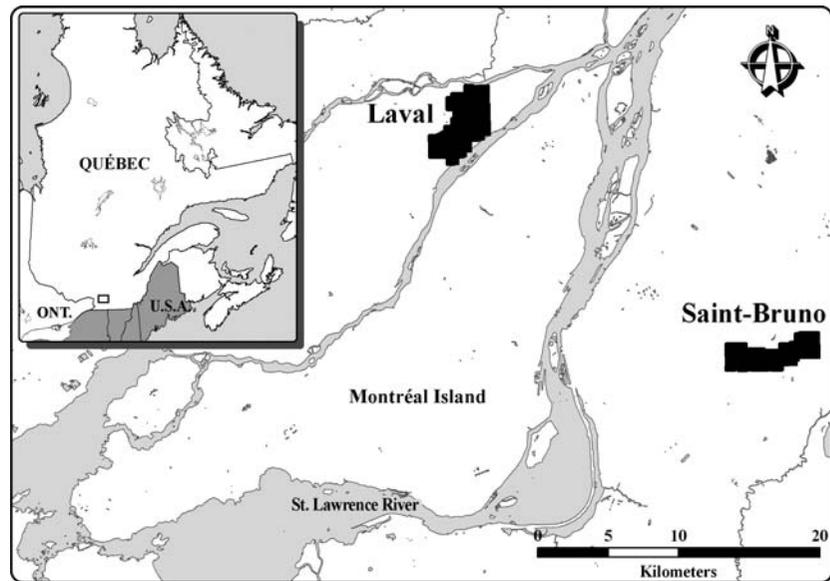
this network was largely put in place in the 1970s when farmers benefited from governmental subsidies to improve drainage conditions (Domon et al. 1993). The proximity of those agro-forested landscapes to the city of Montréal has greatly contributed to increase urbanization pressure in the last two decades.

Data collection

Large-scale aerial photographs were used to reconstruct *P. australis* invasion patterns in all available habitats. Because most of our populations were found within narrow linear wetlands, which can increase mapping errors, we first conducted a thorough accuracy assessment supported by extensive field sampling, according to the methodology proposed by Maheu-Giroux and de Blois (2005). User's accuracy of the most recent images was 84% (i.e., 84% of populations on the map are actually on the ground). Images from 1985 (1/5000; panchromatic), 1988 (1/5000; panchromatic), 1995 (1/10,000; panchromatic), and 2002 (1/8000; color) were available for St-Bruno and from 1987 (1/5000; panchromatic), 1993 (1/10,000; panchromatic), 1995 (1/10,000; panchromatic), 1997 (1/5000; panchromatic), 2001 (1/10,000; panchromatic), and 2002 (1/8000; color) for Laval. Distribution maps of

P. australis and landscape characteristics were interpreted for each available year from aerial photographs, digitized as polygons, and integrated into ArcGIS 9 (Environmental Systems Research Institute Inc., Redlands CA, USA). A total of 236 aerial photographs were scanned, rectified, geo-referenced, and mosaicked to obtain the 10 final photo-maps (St-Bruno has 4 and Laval has 6).

Ten categories of Land-uses/Land-covers were derived from the photo-maps by photo-interpretation: (1) Agricultural, (2) Commercial, (3) Transportation Right-of-Way (ROW), i.e., managed habitats along roads and railways, (4) Forest, (5) Old-Field, (6) Industrial, (7) Water Bodies, i.e., streams and rivers), (8) City Parks and Golf, (9) Residential, and (10) Wet patches. The latter category is loosely defined as areas that maintain a high water table, permanently or occasionally during the year. The complex network of anthropogenic linear wetlands, i.e. roadsides ditches, railroad ditches, agricultural ditches, etc., as well as other natural riparian habitats alongside streams and rivers were digitized as polygons. Soils maps were obtained from the "Institut de Recherche et de Développement en Agroenvironnement" (IRDA) where the original governmental maps (Agriculture Canada 1952, 1991) were digitized.

Landscape characteristics

Both landscapes are mostly agricultural (corn and soybean production in rotation). They differ in their dynamics, soil conditions, degree of colonization by *P. australis*, and date of construction of major roads. To gain information on the landscape context in which invasion was occurring, we quantified for each landscape the differences related to:

(1) Edaphic conditions; we derived from the soil maps the percentage of total area covered by specific drainage conditions (Good, Moderate, Imperfect, Poor, Very Poor) for the two landscapes to test their effect on *P. australis*' spatial distribution. Water availability is possibly the most important edaphic factor affecting *P. australis* distribution (Wilcox et al. 2003; Hudon et al. 2005). Drainage definitions (Lamontagne and Nolin 1997) refer to the internal drainage of the soil and takes principally into account the slope, texture, vertical water flow speed, and retention capacity of the soil.

(2) Length of linear wetlands bordered by shrubs and/or trees; we included this variable because woody vegetation could potentially limit *P. australis* expansion by shading populations.

(3) Network characteristics; to assess the dynamics of the network of linear wetlands, we calculated the length of this network for each available year. The degree of connectivity of the network was estimated using the Gamma index (γ) (Kristensen and Caspersen 2002; Lee 2004). This index describes the extent to which nodes of the network are connected and is calculated by dividing the number of actual links between the nodes by the maximum potential number of links. It can therefore be expressed as percentage of connectivity. More connected networks could be more invaded than less connected ones.

(4) Land use/Land cover changes can affect *P. australis* invasion patterns by creating disturbances or conditions favorable to establishment. In order to describe these changes, we calculated the percentage of the total landscape area covered by each land use/land cover for each time period.

Phragmites australis invasion pattern analysis

We used the logarithmic growth equation, $N = N_0 e^{rt}$, to analyze changes in the total area of *P. australis* for each landscape (where N is the total area of *P. australis* and t is the time difference in years). We solved the equation to obtain r, the intrinsic rate of increase in area of *P. australis*. This equation normalizes area changes which enabled us to compare our observed intrinsic rates to those obtained in other studies. For both landscapes, more than 85% of the centroids of mapped populations were within 15 m of a linear wetland for all years. Rate of spread in all linear wetlands (% of linear wetlands invaded/year) was therefore calculated for each year, landscape, and land use/land cover. To highlight differences in invasion patterns between natural riparian habitats and anthropogenic linear wetlands, we calculated the number of patches of *P. australis* per km in each habitat type. To highlight patterns in roadside habitats, we also computed the number of *P. australis* patches within ROW per km of linear wetlands for both landscapes at the beginning and at the end of the studied period and contrasted them with patterns outside ROW.

Because clonal growth of *P. australis* is said to be the major means of population growth and spread (Mal and Narine 2004), especially at our latitude, we expected to observe mostly the contiguous expansion of existing patches rather than the establishment of new patches away from source populations. A preliminary inspection of distribution maps, however, suggested that the establishment of new distinct patches was more frequent than expected. The spatial patterns of establishment of new patches within linear wetlands relative to source populations were therefore investigated using variants of the cross-*K* Function, a bivariate second-order spatial point pattern analysis, which is an extension of the traditional *K*-Function for bivariate data sets (Ripley 1976). For this analysis, population

polygons were converted to points using their centroids to accommodate the fact that this function used point-referenced data. Centroids do not account for the spatial configuration of *P. australis* patches in linear habitats, but they were our best approximation of the true distance between polygons. Patterns detected at small spatial scale (e.g., the scale of patches) must however be interpreted with care when centroids are used (Wiegand et al. 2006).

The cross-*K* function allowed us to test spatial dependence between colonization events (i.e., the appearance of new distinct *P. australis* patches) and source populations in the previous reference period over a range of spatial scales. It is based on a count of points within a certain distance, *d*, of each point, with *d* taking a range of scales. Mixed patterns of association (aggregation), randomness, or repulsion (regularity) can therefore be detected over space and time (Wiegand and Moloney 2004). We hypothesized that new colonization events would be mostly associated with source populations over relatively short distances and therefore focused on distances up to 500 m. In a linear habitat, however, distances can be calculated in two ways: linearly through the network only, or in two-dimensions, i.e., assuming colonization events are not necessarily constrained by the linear dimension of the network and can occur in adjacent segments of linear wetlands as well. For instance, depending on the spatial structure of the network, the location of a patch relative to another could be measured as 500 m if we follow the network (one dimension), but only 100 m in two-dimensions (bird's flight) if parallel linear segments of the network are 100 m apart. Both distances may account for different dispersal processes (e.g., water transport of rhizomes within the network versus seed dispersal by dominant wind or human-mediated displacement of propagules). In the first instance, the network cross-*K* function (Okabe and Yamada 2001; Spooner et al. 2004a, b; Deckers et al. 2005) was used to calculate distances between points using network (linear) distances (1D). In the second case, the more traditional version of the cross-*K* function calculated the Euclidian (2D) distances between points. Taking into account both types of spatial patterns may allow for a more complete and accurate investigation of colonization events.

The network cross-*K* Function (1D) was computed using an ESRI ArcMap extension, SANET—v 2.0 (Okabe et al. 2004). Confidence envelopes were obtained using 99 Monte Carlo simulations of the null model. Assessing the significance of bivariate point patterns may be problematic because various null models may apply (Wiegand and Moloney 2004). The choice of an appropriate model depends on the biological question asked. The most commonly used null model is complete spatial randomness. In our case, we were interested in assessing whether new colonization events tend to cluster near source populations over time (Wiegand et al. 1998). It is therefore inappropriate to randomize the two patterns of source populations and colonization events since the source populations (antecedent conditions sensu Wiegand and Moloney 2004) have to remain fixed. So we kept the location of the source populations fixed and randomized the location of the colonization events. No edge effect (Haase 1995) adjustments were necessary using the network cross-*K* function since edge effects were intrinsically taken into account in the network distances computations (Okabe and Yamada 2001). For the 2-D cross-*K* Function, we used an *R* package, "Spatstat" (Baddeley and Turner 2005). Confidence envelopes were constructed using the same null model as in the network cross-*K* Function but randomization of the locations of the colonization events were restricted to the network of linear wetlands (i.e., we did not allow a colonization event to be located in the middle of a road/agricultural fields/etc.). This suited better the assumption of environmental homogeneity (stationarity of the point pattern) of the *K* function. To correct for edge effect, we used the translation correction (Ohser 1983). Because there were too few colonization events from 1985 to 1988 in St-Bruno, we excluded this time period from this analysis.

Predictive model of *Phragmites australis* occurrence at the landscape scale

For the most recent surveyed year (2002), the presence/absence of *P. australis* in the network of

linear wetlands was modeled using land use/land cover and landscape characteristics. The networks of each landscape were first divided in 32,053 10-m long segments (19,253 segments for Laval and 12,797 segments for St-Bruno) and each segment was assigned presence/absence data for *P. australis*. The mutually non-exclusive land uses/land covers tested are: (1) Agricultural, (2) Transportation ROW, (3) Urban areas (industrial, commercial, golf, city park, and residential areas), (4) Old-field, (5) Forest, (6) Water bodies, and (7) Wet patches. We also included land use/land cover changes from the beginning of the observation period to the last year observed. Changes in specific land use/land cover were grouped into broader categories and coded as binary variables: (8) Agricultural intensification (e.g., old-fields returned to cultivation), (9) Land abandonment (agricultural field abandoned), (10) Urbanization, (11) Road constructions and road work (e.g., road enlargement), and (12) a disturbance category that included all major soil disturbances (such as demolition of a chemical plant) and changes in hydrology (such as creation of wet patches resulting from culvert blockage). The Euclidian distance to a ROW (13) was also recorded for each segment. To accommodate possible non-linear responses for the distance variable, we also tested its square and cubic terms. Finally, drainage conditions (14) at the center of the segment obtained from the soil maps and the presence of woody vegetation (15) for each segment were tested in the regression. None of the variables exhibited strong multicolinearity (defined as Variation Inflation Factor ≥5), except for the linear, square, and cubic terms of the distance to a road, which was expected.

Preliminary analyses modeling the occurrence of *P. australis* using multiple logistic regressions demonstrated that the residuals were highly positively autocorrelated at short distances, which was to be expected for a highly clonal species in linear habitats. This lack of independence between pairs of neighboring observations violates the independence assumption of classical tests of significance (Legendre 1993; Legendre and Fortin 1989). Moreover, ignoring spatial autocorrelation generally leads to an overestimation of habitat effects (Klute et al. 2002; Lichstein et al. 2002;

Betts et al. 2006). A way to account for spatial dependence is to use an autologistic regression model (Augustin et al. 1996; Gumpertz et al. 2000; Keitt et al. 2002; Klute et al. 2002; Lichstein et al. 2002; Betts et al. 2006). Autologistic regression includes spatial autocorrelation in the model by adding an autocovariate. The autocovariate conditions the response, for a given observation, on the response of observations in neighboring locations. We determined the number of neighboring observations to include in the calculation of the autocovariate by successively including neighbors at a threshold (Euclidean) distance ranging from 10 to 600 m, at increments of 10 m from 10 to 100 and increments of 50 m afterwards. We used a threshold of 600 m because we expected autocorrelation mostly at short distances according to our preliminary analyses. Increments of 10 m were chosen because it corresponds to the distance between adjacent observations in the networks of linear wetlands. The autocovariate that produced the most parsimonious autologistic model for each landscape, i.e., that minimizes the Akaike Information Criterion (Akaike 1973), corresponds to a threshold distance of 20 m for both landscapes. Interestingly, because parallel segments of linear wetlands are generally more than 25 m apart, the Euclidian distance threshold accounts mostly for patterns within the linear network and could be equivalent to using a network distance.

Computational limitations prevented us from using all observations to test our model as the distance matrix would be too large (32,053 *32,053 elements). Thus, we tested our model for each landscape separately and by sub-sampling the landscapes. All observations where *P. australis* is present needed to be included in the sample to calculate the autocovariate. Therefore, we randomly chose for inclusion in our model an equivalent number of observations without *P. australis*. Autologistic regressions (for St-Bruno, $n = 3,962$; for Laval, $n = 1,580$) were performed using SAS 9.1 (SAS Institute Inc., Cary, NC, USA) and variables were selected using the stepwise selection procedure. The Wald statistic was used to test the significance of the regression criterion and Nagelkerke R^2 (Nagelkerke 1991), a coefficient of determination for logistic regression, was used to

assess the model goodness of fit. Autocorrelation of the Pearson residuals was investigated using Moran's *I* (Moran 1950) and significance was assessed using 999 permutations. The progressive Bonferroni correction was used to account for multiple tests (Hewitt et al. 1997). Inspections of Moran's *I* correlograms of regression residuals for both landscapes confirmed that autocorrelation was very well accounted for in the autologistic models.

Results

Landscape characteristics

Drainage conditions in St-Bruno differ from the ones in Laval. Poor drainage conditions occupy 79% of the St-Bruno landscape, whereas 69% of the total area shows a moderate drainage in Laval (Fig. 2). Linear wetlands with woody vegetation represent 5% of the network length in St-Bruno compared to 19% in Laval. The linear wetland networks of both landscapes have increased in length at the beginning of the time period with a maximum attained in 1988 for St-Bruno (154 km) and in 1993 for Laval (234 km) (Table 1). Increases in network length are mostly due to the drainage of former old-fields for agricultural purposes in St-Bruno and by the construction of a new road in Laval. After reaching a peak, the length of networks

Fig. 2 Drainage conditions of the St-Bruno and Laval landscapes

decreases by about 14% in each landscape. In St-Bruno this decrease is caused mostly by residential construction and in Laval by residential constructions and the filling of drainage ditches after agricultural abandonment. Regarding the connectivity of the two networks, the γ index shows that 39.6% of all nodes are connected in St-Bruno at the beginning of the reference period (Table 1). After that, connectivity decreases continuously to a low of 36.2% of nodes connected. In Laval, the maximum connectivity is 40.5%, attained in 1993 after the new road was constructed. Subsequently, the degree of connectivity diminished to 38.8% in 2001, followed by a small increase in 2002. Although, the degree of connectivity is slightly higher in Laval, the mean link length is smaller in St-Bruno (170 vs. 124 m in 2002, respectively). Thus, even if the Laval network is more connected, longer distances need to be traveled before finding a connection.

At the beginning of the studied period, a more agricultural and forested landscape was present in St-Bruno (Fig. 3). Changes occurred primarily through urbanization (industrial, commercial, and residential) and the shift of old-fields or agricultural areas to city parks and golf courses. Wet patches have seen their areas increased until 1995, when they were filled following urbanization. Laval has seen its landscape shift from old-field and industrial zones to urbanized (residential and commercial) and agricultural areas (Fig. 4). Some old-fields were also left undisturbed and became forested. A road (4.6 km) was also constructed on agricultural fields and forested areas in 1989. The increase in wet patches between 1997 and 2001 is due to the blockage of railroad culverts which has caused the flooding of old-fields.

Phragmites australis invasion patterns

St-Bruno exhibited a severe invasion in 2002 and the rapidity of *P. australis* spread is impressive (Fig. 5). The pattern of invasion was less severe in Laval (11.8% of total network length invaded for St-Bruno versus 2.5% in Laval) mostly because agricultural areas are less invaded (Fig. 6). The two landscapes were relatively non-invaded at the
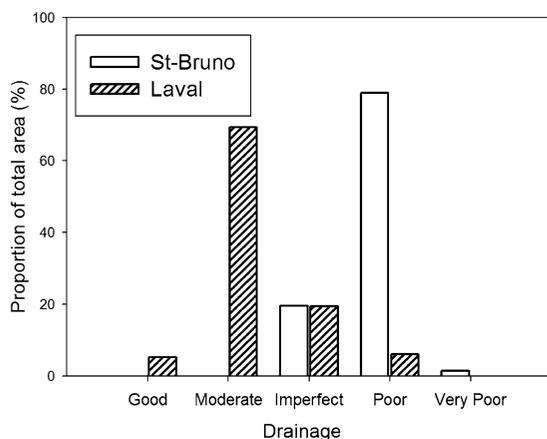
Table 1 Total network lengths (km) and gamma connectivity index (γ) for the network of linear habitats in each landscape

St-Bruno			Laval		
Date	Length (km)	Gamma index	Date	Length (km)	Gamma index
			1987	212.7	0.40
1985	147.7	0.40	1993	234.6	0.41
1988	154.1	0.38	1995	222.6	0.40
1995	153.8	0.38	1997	202.1	0.39
2002	133.5	0.36	2001	203.4	0.39
			2002	202.3	0.39

Fig. 3 Land-uses/land-covers proportions at each time observation in the St-Bruno landscape
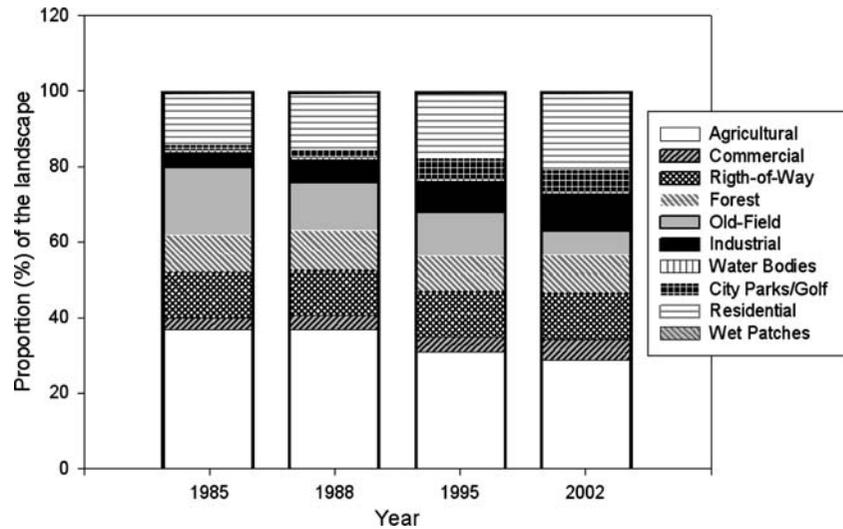

Fig. 4 Land-uses/land-covers proportions at each time observation in the Laval landscape
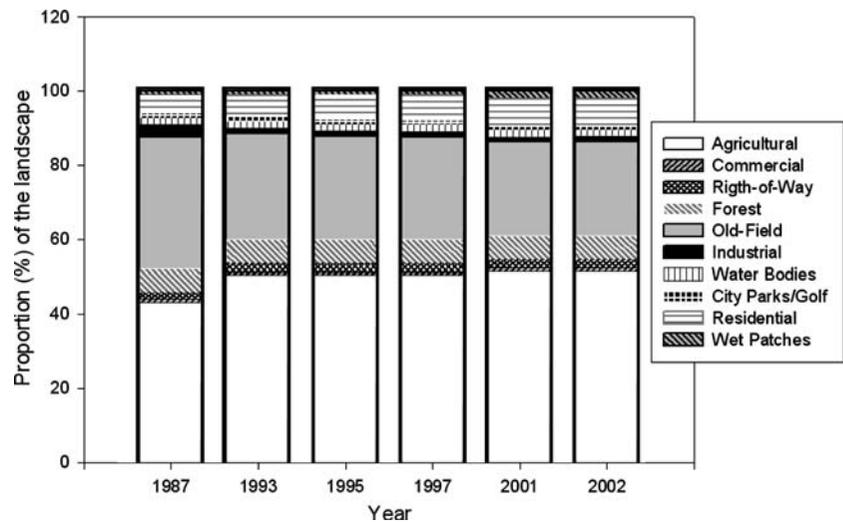
beginning of the reference period and populations occurred mostly near ROW at that time (Fig. 7). In both landscapes, invasion therefore occurred first in roadsides habitats then in other linear wetlands, such as those that intersect agricultural areas (Figs. 5, 6).

Fig. 5 Distribution maps of *P. australis* for the St-Bruno landscape
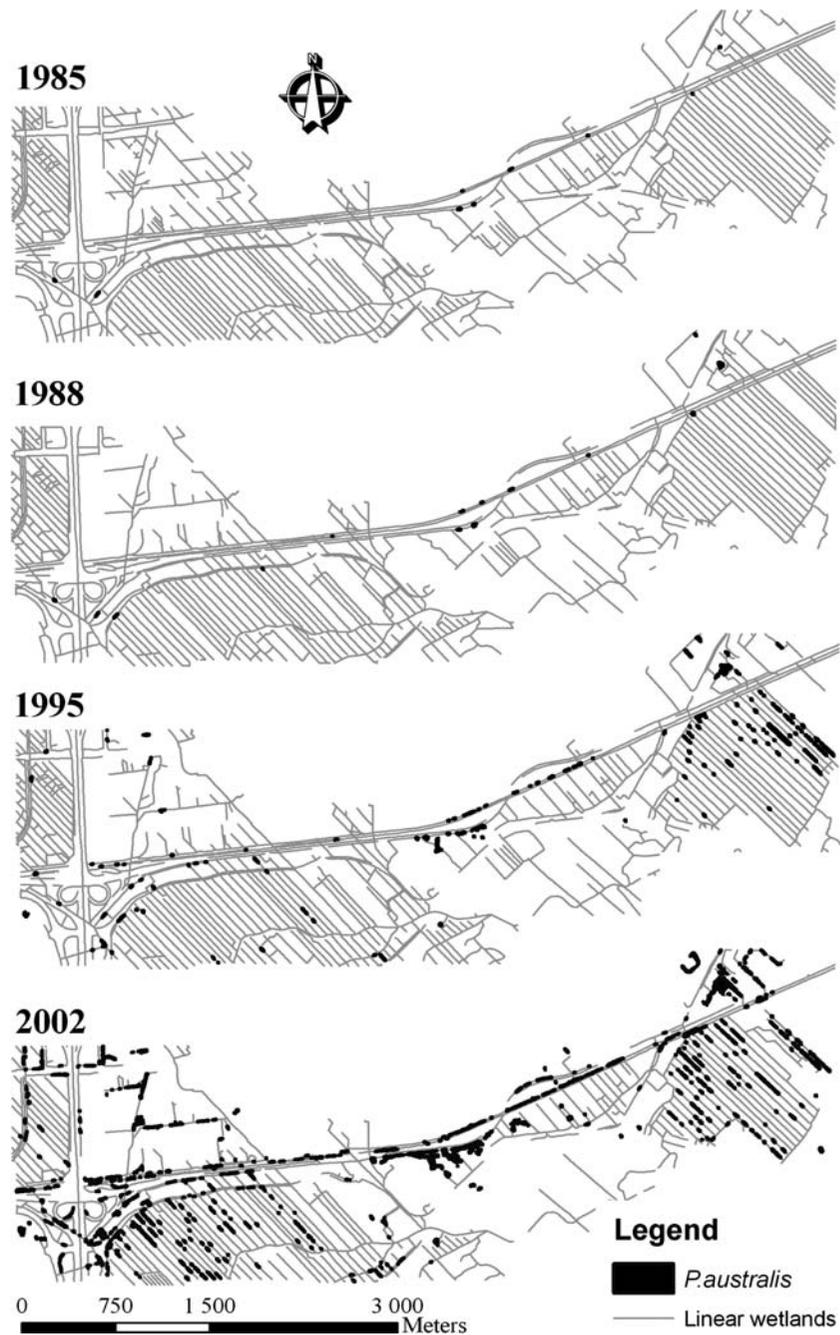
The annual intrinsic rate of increase of *P. australis* for each landscape was high (Table 2). Maximum intrinsic rates of increase were observed after the initial establishment of the first populations in both landscapes and decreased afterward. The overall rates of invasion in our habitats appear to exceed those generally reported for natural wetlands even if lateral growth of populations is constrained within linear wetlands (Table 3). At the high end, though, our observations overlap with those calculated at Long Point in Lake Erie (Ontario, Canada)

Fig. 6 Distribution maps of *P. australis* in the Laval landscape (maps for 1995 and 2001 are not represented)

Legend

■ *P. australis*

— Linear wetlands

0   750   1 500   3 000
                              Meters
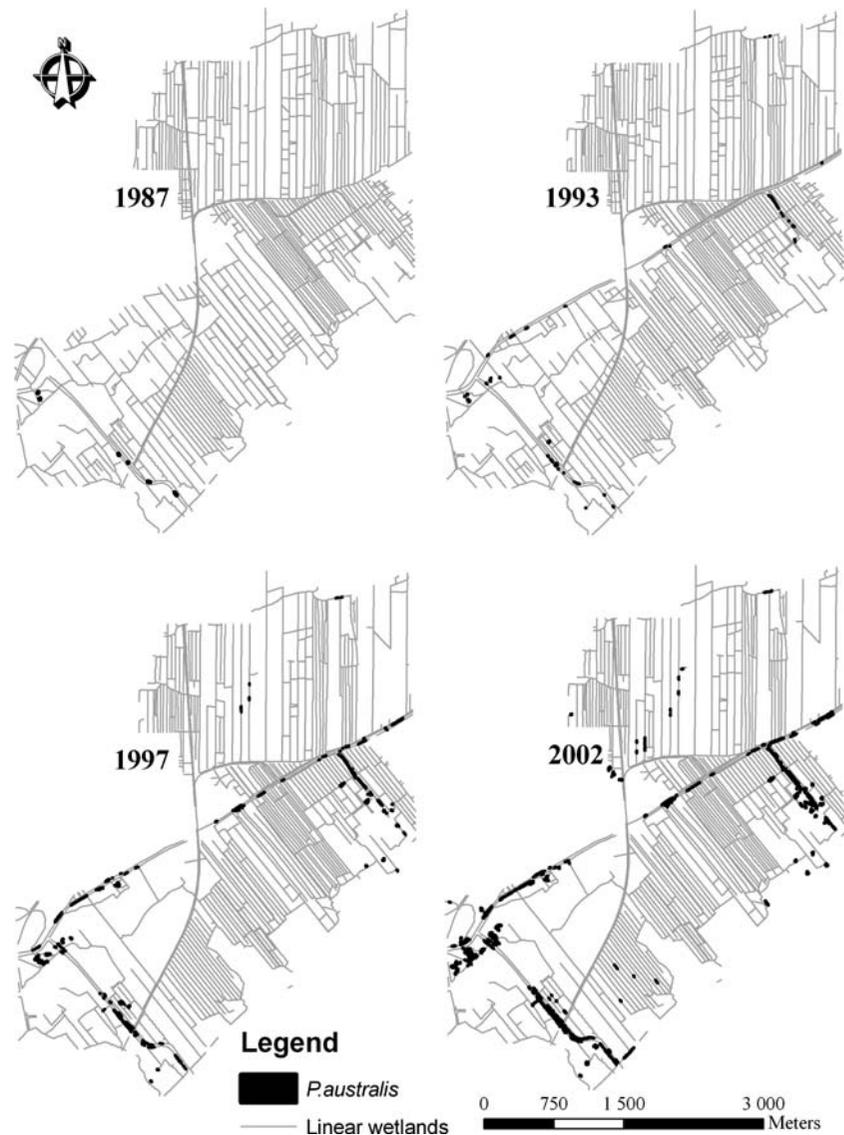
where rates of increase are highly variable, ranging from − 0.74 to 0.50 year^{-1} (Wilcox et al. 2003).

Interestingly, in both landscapes riparian habitats were little invaded compared to anthropogenic linear wetlands. When we excluded riparian habitats that intersect transportation ROW, 0.07 patches of *P. australis* per km were found in riparian habitats versus 1.96 patches in anthropogenic linear wetlands. When riparian habitats intersect ROW, however, they tend to be more invaded (1.15 patches of *P. australis* per km in riparian habitats including those that intersect ROW versus 1.96 in linear wetlands).

Depending on landscape context, the linear structures show different extent of invasion. In St-Bruno, linear wetlands within commercial areas were the most invaded landscape elements (40% of their length invaded in 2002) but they only represent 1.5% of all linear wetlands (Fig. 8). Industrial (16% in 2002) and transportation ROW (13% in 2002) followed. ROW, however, represent 30% of all linear wetlands in St-Bruno. Other linear structures invaded were within agricultural (8.5% in 2002), residential (6% in 2002), forest (1.5% in 2002), and old-field (1%) areas. In Laval, the transportation ROW were the most invaded linear elements (22.5% in 2002) and
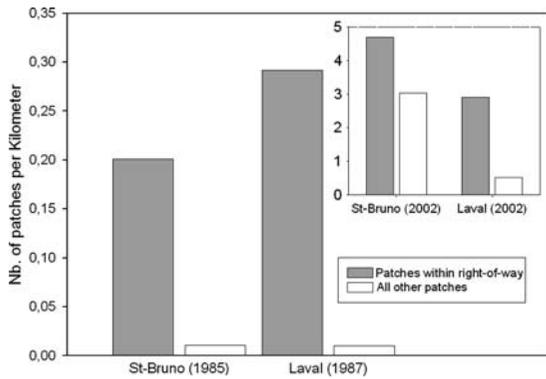
Fig. 7 Number of patches of *P. australis* per km of linear wetlands within transportation rights-of-way compared to patches within other land use/land cover contexts, at the beginning and end of the study period for each landscape

they represent 7.3% of all linear wetlands of this landscape. Linear wetlands situated in old-fields (3.5% in 2002) and in agricultural fields (< 1%) are also invaded. Most of the invaded old-fields in the Laval landscape were situated near an industrial plant that was demolished.

Colonization events in St-Bruno occurred at a yearly mean Euclidian distance of 105 m/year,

and at a yearly mean distance of 115 m/year at Laval, but these estimates are skewed by rare long-distance events. If the top 5% longest dispersal events are removed, establishment occurred at a mean distance of 27 m/year in St-Bruno and 77 m/year in Laval. The lower distance dispersal of St-Bruno is caused by the fact that distances are calculated from the closest source population. Therefore, the higher population density of St-Bruno is affecting the estimates.

Cross-*K* Function analysis revealed that colonization events were generally aggregated with source populations both using network and Euclidean distances, although the spatial scale at which association occurs varied with time (Fig. 9). In general, aggregation at St-Bruno tends to be observed at larger spatial scales (around 100–500 m) than at Laval (around 20–50 m up to 500 m). At Laval, patterns measured with network distances tend to be similar to patterns measured with Euclidian distances, but this is less the case at St-Bruno, where patterns based on Euclidian distances are generally less significant than network patterns.

Table 2 Intrinsic rates of increase (year^{-1}) for populations of both landscapes

| St-Bruno		Laval	
Time periods	Intrinsic rate of increase	Time periods	Intrinsic rate of increase
		1987–1993	0.4308
1985–1988	0.3438	1993–1995	0.5400
1988–1995	0.3632	1995–1997	0.4394
1995–2002	0.1957	1997–2001	0.2590
		2001–2002	0.1900

Table 3 Comparisons of observed intrinsic rates of increase in linear wetlands with the ones reported for natural wetlands in the literature

Region	Salinity	Intrinsic rates of increase (year^{-1})		References
		Minimum	Maximum	
Montréal, Québec (Canada)—Linear wetlands	*Freshwater*	*0.1900*	*0.5400*	*(This study)*
Chesapeake Bay (USA)	Freshwater/Oligohaline	0.0065	0.2123	Rice et al. (2000)
Delaware, New Jersey, and New York (USA)	Brackish	0.0024	0.2537	Lathrop et al. (2003)
Lake Erie, Ontario (Canada)	Freshwater	–0.7400	0.5000	Wilcox et al. (2003)
Saint-Lawrence River, Québec (Canada)	Freshwater	0.0477	0.2100	Hudon et al. (2005)*

*Calculated from the data included in the cited article
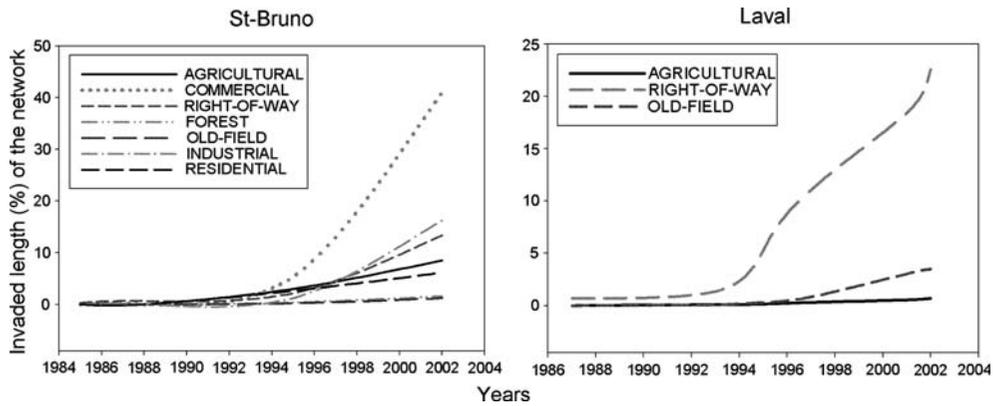
Fig. 8 Rate of invasion of different land-uses/land-covers for both landscapes
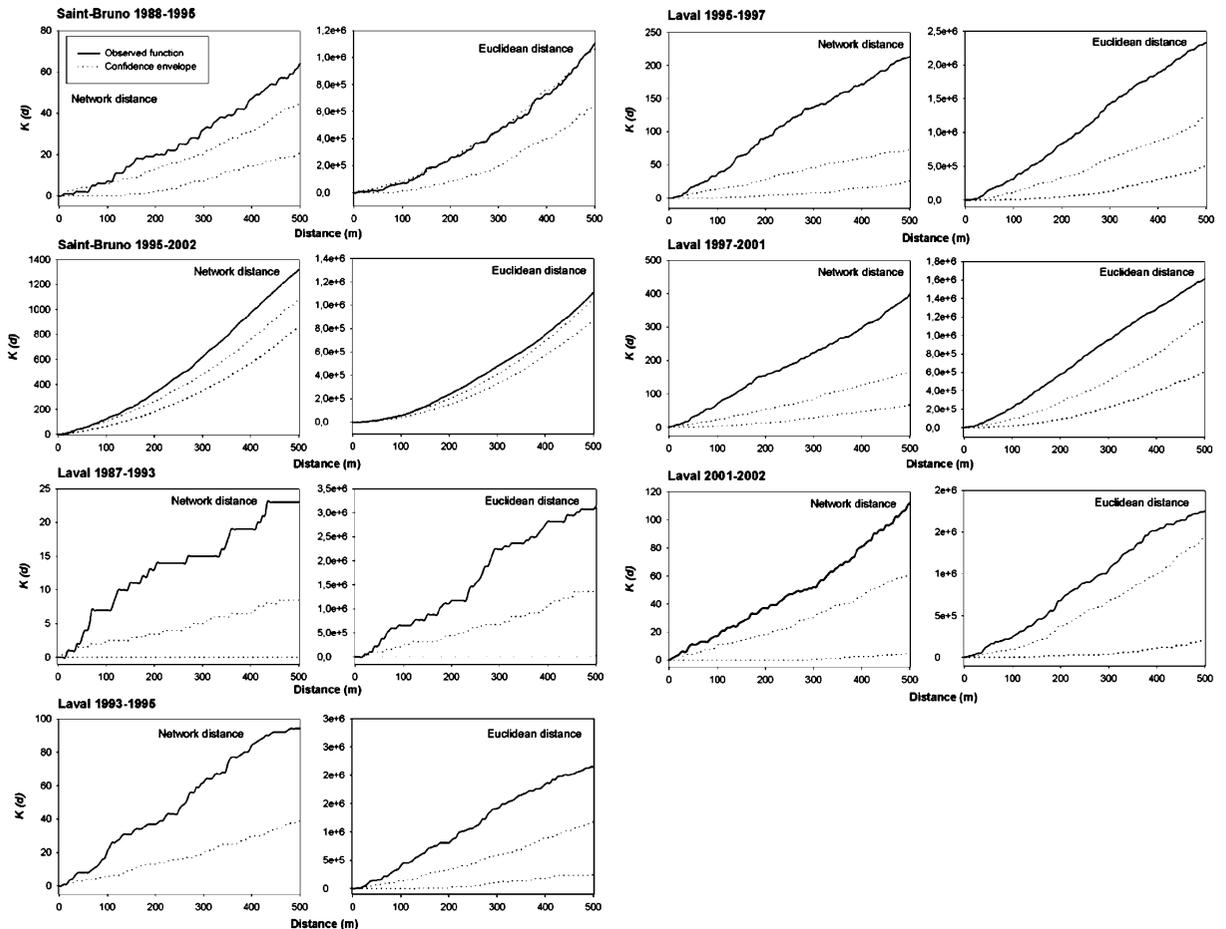
Fig. 9 Spatial dependence of colonization events to source populations over time and a range of spatial scales as determined by the bivariate version of the Rypley's K using network and Euclidean distances for the two landscapes. When the observed curve is above the calculated confidence envelopes, aggregation is observed. When the curve is in between, the spatial patterns are random and when it is below, repulsion (or regularity) is observed

Predictive model of *Phragmites australis* occurrence at the landscape scale

For the St-Bruno landscape, the stepwise selection procedure only retained the autocovariate (score $X^2 = 1311.98$, $P \leq 0.0001$) and the resulting model is:

$$P. AUSTRALIS = \text{INTERCEPT} + 6.5284$$
$$(\text{AUTOCOVARIATE})$$

This model accurately predicted 92.0% of our observations and Nagelkerke R^2 was 0.82.

For the Laval landscape the stepwise selection procedure retained the following variables: the land use/land cover "Transportation Right-of-Way" (score $X^2 = 15.18$, $P \leq 0.0001$) and the autocovariate (score $X^2 = 327.81$, $P \leq 0.0001$). The model is:

$$P.AUSTRALIS = \text{INTERCEPT} + 1.6553$$
$$(\text{TRANSPORTATION}$$
$$\text{RIGHT-OF-WAY})$$
$$+ 8.1408 (\text{AUTOCOVARIATE})$$

For this landscape, the probability ($P = \log(P.\ australis/(1 - P.\ australis))$) of finding a population of *P. australis* increases if the segment is located within a transportation right-of-way. This model accurately predicted 98.1% of our observations and Nagelkerke R^2 was 0.94.

Discussion

Because they intersect various land-uses, linear habitats have the potential to serve as invasion corridors facilitating the spread of *P. australis* at the landscape scale. Our results show that transportation ROW were more likely to drive invasion patterns, serving as invasion foci into other parts of the landscapes. Roadside ditches, in particular, act, like wetlands (Zedler and Kercher 2004), as sinks that collect nutrients, sediments, and salts from the surrounding land-uses. They connect to most other types of linear wetlands, especially agricultural ditches which can be an important source of phosphorus in these

landscapes dominated by corn cultivation (Beauchemin et al. 1998; Jamieson et al. 2003). For instance, road construction at Laval contributed to increase linear habitat connectivity. Roadside ditches also connect to other roadside habitats outside of our landscapes' boundaries which could have served as sources of propagules into our landscapes. Roadside habitats also receive salts from road maintenance operations to which the exotic genotype of *P. australis* appears to be tolerant (Vasquez et al. 2005) and which could reduce competition from other species in these habitats.

Phragmites australis is considered a nuisance when it competes with native species or alters ecosystem functions in natural wetlands (Weinstein and Balletto 1999). In linear habitats, it may just act as an obvious indicator of eutrophication and may serve to capture, at least temporarily, the heavy load of nutrients and herbicides before they reach aquatic ecosystems (Sun et al. 1999; Naylor et al. 2003; Schroder et al. 2005). This "ecosystem service" may come at the cost of saturating the landscape with propagules that will eventually reach more pristine wetlands. Interestingly, the riparian habitats of slow streams and rivers, even though they seemed in most instances suitable, were not colonized by *P. australis*, except when they intersected transportation ROW. It is possible that differences in disturbance and hydrological regimes or competitive vegetation in the riparian habitats contribute to limit invasion. These differences are worth investigating in the field because they may suggest potential control strategies using other native competitive species (de Blois et al. 2004), or they may suggest ways to mitigate invasion along natural areas when they intersect roads.

The overall rates of increase in our linear habitats appear to generally exceed those reported for natural wetlands, which suggest again highly appropriate ecological and spatial conditions for recruitment and growth in linear wetlands. Intrinsic rates of increase vary with time and changes in hydrological conditions. Wilcox et al. (2003), for instance, report comparatively high intrinsic rates of increase of *P. australis* in natural wetlands possibly as a response to water levels in Lake Erie well below long-term average. Hudon et al. (2005), who conducted their study in

riverine wetlands from the same hydrographic region than ours, observed that elevation could limit *P. australis* growth in some sections of their wetlands. Elevation at the scale of our study was not variable enough to test its effect, but hydrological conditions in our linear wetlands will result in water level fluctuation that could greatly favor *P. australis* establishment and growth.

The different types of land uses/land covers that we considered correspond to different management units, from minimal to no intervention along abandoned fields to possibly aggressive management in agricultural ditches (cut, burn, herbicide drift). The extent to and the rate at which linear wetlands of different landscape elements are invaded may reflect the degree of disturbances or control to which they are submitted. Observing these patterns can also provide insights into future trends. For instance, industrial areas that have been heavily disturbed and then abandoned in Laval show a high extent of invasion. On the other hand, agricultural ditches in Laval are relatively non-invaded compared to agricultural areas of St Bruno, where none of the variables included in our predictive model was significant. We expected differences in drainage conditions to play a role, but this was not supported by the autologistic models at the landscape scale, possibly because ditches show highly modified edaphic conditions. Because they are highly connected, linear wetlands would also tend to reflect conditions from all parts of the landscape, not just from adjacent land uses, which could have prevented the detection of landscape effects at the scale of our analysis. It could be informative in this case to test for the effect of differences in the internal structure of the drainage ditches (width, depth, etc.) or differences in management practices by farmers. Since both landscapes tend to support similar intensive crops, our results suggest that it could be only a matter of time until we observed similar patterns of invasion in agricultural land in Laval. Given the speed at which the populations have spread in the past, it may therefore be important to control even the smallest patches to avoid having to deal with populations that will eventually be beyond control.

We expected colonization events to be generally aggregated to source populations and this is corroborated by the results of point pattern analysis in both landscapes. We detected scale dependence that could be related to the spatial configuration of the network itself and to the time lag between observations, especially at St-Bruno. The distances at which we detected association patterns are generally quite similar using both types of distances (Euclidian or network) at Laval, but differ between the two types of distances used for St. Bruno where a greater portion of the landscape is invaded. The longer time lag between observations at St Bruno (7 years) could have obscured the small scale spatial signal since numerous intermediate (i.e., non-observed) colonization events occurred in all parts of the landscape during the exponential phase of invasion, resulting in aggregation observed at larger spatial scales. Moreover, patterns of invasion are more complex in St-Bruno where ditches are also separated by larger distances, and aggregation seems to be better accounted for by linear (1D) distances, with random or near random colonization across different segments of the network. This suggests that the transport of propagules, likely facilitated by water, is more predictable within than across ditches. In Laval, colonization was largely restrained to roadside habitats (Fig. 4) and this explains the similarity between the two functions and the strong spatial dependence observed.

In any cases, spatial analysis and invasion maps showed a high number of colonization events both within and across ditches. Although vegetative propagation certainly plays a role in these colonization events, these patterns also raise questions about the contribution of sexual reproduction which have not been previously investigated in these habitats. It is generally assumed that sexual reproduction is extremely variable between populations and between years and rare in many populations (Mal and Narine 2004), especially at our latitude. In fact, well-resourced plants, such as the ones thriving in eutrophic linear wetlands, may produce more seeds (Mckee and Richards 1996) than populations in natural wetland habitats that are resource limited. Germination tests (following the methodology of Ekstam and Forseby 1999) performed on our populations demonstrated that they

produced viable seeds in a proportion of 6.6% in St-Bruno (maximum is 27.1%) and 2.7% in Laval (maximum is 11.3%). Given that each inflorescence can produce large amounts of seeds of which an average of 350–800 per inflorescence would be viable in our populations, the contribution of sexual reproduction in the establishment of new patches could be more important than previously thought, especially since seeds tend to colonize bare soils (Ailstock et al. 2001), but this remains to be tested in linear habitats. The very small abundant seeds of *P. australis* can be transported large distances from their sources by wind, which could result in random or nearly random patterns especially using Euclidian distances. It is possible that more prolific populations at St-Bruno have greatly contributed to a greater invasion extent in this landscape.

If invasibility increases with increased propagule pressure (Foxcroft et al. 2004; Rouget and Richardson 2003), highly interconnected linear wetlands well fed by agricultural runoffs such as the ones described in this study have a high probability to serve as a source of propagules for intersected natural wetlands, perhaps especially when vegetation in these wetlands is disturbed. This hypothesis has been partly verified by our data on the interaction between transportation ROW and riparian habitats, but we would need more evidence at the regional scale to corroborate these findings. Moreover, given the trends observed in this study, new transportation rights-of-way will have a very high chance to be invaded, especially when they connect to segments that are already invaded. As for other linear wetlands such as agricultural ditches, they should be monitored carefully and managers should act as early as possible if they want to limit expansion to acceptable level given the high invasion rates observed. Active and repeated control interventions at early stages of invasion may be the only way to mitigate the negative impact of the species on natural and anthropogenic wetlands, but in many instances this option will require significant efforts given the stronghold *P. australis* already has on linear habitats.

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