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Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens

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Abstract

Aim To reconstruct the spread of invasive wetland species using herbarium specimens and to develop a method that accounts for the biases associated with this type of historical record.

Location Southern Québec.

Methods The temporal and spatial distribution of herbarium specimens of vascular plants was examined. Six invasive species that are mainly found in wetlands were compared with five native, non-expanding hydrophytes. The cumulative number of locations was plotted against time to construct invasion curves. For native species, this 'invasion curve' indicates the spatiotemporal distribution of the sampling for herbarium specimens of wetland plants. It also represents the history of the state of knowledge of the distribution of native species. Deviation from the native species invasion curve can be used to describe the spread of invasive species. For every year on record, the cumulative number of locations of each exotic species was divided by the cumulative number of locations of all native species, and the proportions obtained were plotted against time. Periods of invasiveness were then delineated.

Results During the twentieth century, two periods of intensive herbarium specimen collection in Québec can be clearly distinguished, i.e. from 1930 to 1940 and from 1950 to 1985. Several periods of invasiveness were delineated for *Butomus umbellatus* L. (1922–35), *Hydrocharis morsus-ranae* L. (1957–96), *Lycopus europaeus* L. (1963–2000), *Lythrum salicaria* L. (1890–1905, 1923–46), *Phragmites australis* (Cav.) Trin. ex Steudel (1963–84) and *Rorippa amphibia* (L.) Bess. (1929–34, 1943–52, 1971–79).

Main conclusions Accounting for sampling biases associated with herbarium specimens is important in order to objectively delineate periods of invasiveness for exotic species. The spread of wetland vascular plant species can be reconstructed using herbarium specimens, even when the phenomenon is rapid, but the reconstruction is certainly more accurate when the invasion occurred during an active sampling period. The highly variable sampling effort for herbarium specimens in Québec and in other regions strongly cautions against using herbarium data without correction procedures.

Keywords
Butomus umbellatus, herbarium specimen, *Hydrocharis morsus-ranae*, invasive species, *Lycopus europaeus*, *Lythrum salicaria*, *Phragmites australis*, *Rorippa amphibia*, St Lawrence River, wetland.

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INTRODUCTION

A large number of botanists and ecologists use herbarium specimens to analyse the temporal and spatial dynamics of phytogeographical phenomena. Plant specimens stored in herbaria are usually well preserved, so any identification error can be corrected to account for recent progress in taxonomy. Furthermore, each specimen includes a label with rich information about sampling location and date as well as associated habitat. Herbarium specimens have been used to define conservation priorities (MacDougall *et al.*, 1998), to document species decline (Hedenäs *et al.*, 2002), and especially to reconstruct biological invasions (Stuckey, 1980; Reznicek & Catling, 1987; Pyšek, 1991; Pyšek & Prach, 1993, 1995; Catling & Porebski, 1995; Weber, 1998; Lambrinos, 2001; Mihulka & Pyšek, 2001). However, the use of herbarium specimens suffers from several biases including identification problems in the field, accessibility of sampling sites, seasonality of plant growth and variability of sampling effort over a long time period. Some groups of species, such as aliens or garden escapes, are recorded less consistently than native species (Rich & Woodruff, 1992; Rich & Smith, 1996; Urmi & Schnyder, 2000). Even regions with strong floristic traditions like the British Isles or the Czech Republic are not free from such biases (Rich & Woodruff, 1992; Mihulka & Pyšek, 2001; Pyšek *et al.*, 2002).

There have been very few attempts to correct for the biases associated with herbarium specimens. Mihulka & Pyšek (2001) standardized herbarium data with respect to the intensity of floristic research in a given country. While this method is reliable for comparing the history of plant species invasion between countries, it assumes that the sampling effort remains constant over time for all species groups, which is rarely the case (MacDougall *et al.*, 1998; Hedenäs *et al.*, 2002). Hedenäs *et al.* (2002) randomly picked specimens in a herbarium and evaluated how the collecting frequency of a species changed in relation to the number of random samples collected during a particular time period. This method is efficient for documenting species decline but is inappropriate for reconstructing biological invasions because the spatial aspect of data is neglected.

In this study, we developed a new herbarium-based method of reconstructing the spread of invasive species. This method accounts for some of the biases associated with herbarium specimens. This method is based on previous work by Petr Pyšek and collaborators (Academy of Sciences of the Czech Republic) and is particularly suited to regions with a recent floristic tradition and/or with a high variability of sampling effort over time. We compared the sampling and spatial distribution of herbarium specimens of six invasive vascular plants (*sensu* Richardson *et al.*, 2000) that are mainly found in wetlands to those of five native, non-expanding hydrophytes. Reconstructing the spread of invasive wetland species using herbarium specimens presents a challenge because rivers function as corridors for plant dispersal (Pyšek & Prach, 1993; Johansson *et al.*, 1996). Consequently, the spread of such species is usually a very rapid phenomenon (Stuckey, 1980; Lonsdale, 1993; Catling & Porebski, 1995; Lachance & Lavoie, 2002) that might not be tracked correctly by herbarium records.

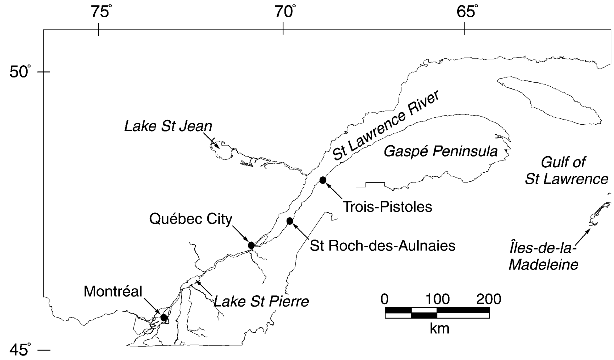

Figure 1 Study area (southern Québec, Canada), with place names cited in the text.

METHODS

We reconstructed the spread of wetland plant species in the province of Québec, Canada. The focus of this study was dictated by three factors: (1) several invasive wetland plants were first introduced in North America along the St Lawrence River, which crosses the south-western part of the province (Fig. 1), (2) the floristic tradition in Québec is quite recent and the degree of sampling for herbarium specimens has been highly variable during the last two centuries, thereby emphasizing the need for a method that accounts for biases associated with botanical surveys, and (3) we had easy access to herbarium specimens stored in the province. To develop our method, we selected six vascular plant species that are known to be moderately to highly invasive in the wetlands of north-eastern North America (Thompson *et al.*, 1987; White *et al.*, 1993; Catling & Porebski, 1995; Chambers *et al.*, 1999; Lachance & Lavoie, 2002; Lavoie *et al.*, 2003): (1) *Butomus umbellatus* L. (Butomaceae), (2) *Hydrocharis morsus-ranae* L. (Hydrocharitaceae), (3) *Lycopus europaeus* L. (Labiatae), (4) *Lythrum salicaria* L. (Lythraceae), (5) *Phragmites australis* (Cav.) Trin. ex Steudel (Gramineae) and (6) *Rorippa amphibia* (L.) Bess (Cruciferae). All species are exotics from Eurasia, except *P. australis*. However, there are strong evidences that the recent expansion of the cover and distribution of *P. australis* in North American wetlands is the result of a non-native genotype (Saltonstall, 2002). Consequently, we have considered *P. australis* as an exotic in this study. We also selected five native, non-expanding species that are widely distributed in the wetlands of north-eastern North America: (1) *Caltha palustris* L. (Ranunculaceae), (2) *Glaux maritima* L. (Primulaceae), (3) *Lemna minor* L. (Lemnaceae), (4) *Lysimachia terrestris* (L.) BSP. (Primulaceae) and (5) *Spartina pectinata* Link (Gramineae). We hypothesized that compiling their herbarium records would provide a realistic picture of the degree of sampling for wetland plants in Québec during the last two centuries.

We consulted the specimens of the selected species that are stored in the five main herbaria of Québec (MT, MTMG, QFA, QUE and SFS) and in the two herbaria of the Canadian Government (CAN and DAO). Each herbarium specimen was checked for possible misidentification, and the specimen number, sampling location, year of sampling, and habitat characteristics were recorded. Any duplicates and specimens with imprecise information about sampling location or date were discarded. Only specimens collected in Québec were examined.

Data on selected specimens (sampling location and date) were incorporated into a geographical information system (GIS), MapInfo Professional© (MapInfo Corporation, 2001). Using the GIS, we superimposed a 10×10-km grid on a map of Québec. For exotic species, we recorded the first mention of a herbarium specimen in each 10×10-km^2. We repeated the same procedure for native species, but the presence of any one of the five species in a 10×10-km^2 was enough to consider the square occupied, i.e. certainly surveyed by a botanist. For each exotic species and for the native species group, we then plotted the cumulative number of occupied 10×10-km^2 against time to construct an invasion curve (*sensu* Pyšek & Prach, 1993). For native species, this 'invasion curve' indicates the spatiotemporal distribution of the sampling for herbarium specimens of wetland plants in Québec during the last 130 years, i.e. the period during which almost all specimens were collected. It also represents the history of the state of knowledge of the distribution of native species.

Linear regression models were fitted to the logarithm of the cumulative number of occupied 10×10-km^2 against time and the slope b was used as a measure of the invasion rate (Mihulka & Pyšek, 2001). The difference between the slope of each exotic species and that of all native species was tested using a t-test of parallelism of regression lines (Zar, 1996). The Bonferroni's correction was applied to weight the significance level ($\alpha = 0.01$) by the number of t-tests used (Harris, 1975). In principle, the more abrupt the slope of the invasion curve, the more rapidly the invasive species has spread (Pyšek & Prach, 1993). However, this is not necessarily the case in regions where the sampling effort is not constant over time: an abrupt slope may simply mean that during a limited time period, botanists were more numerous in the field and recorded a large number of additional locations for some plant species. Moreover, the slope only gives a global estimation of the invasion rate, and cannot be used to distinguish periods with different levels of invasiveness.

To gain another perspective on the invasion process, we accounted for the variability of the sampling effort: for every year on record, we divided the cumulative number of 10×10-km^2 for each exotic species by the cumulative number of squares occupied by native species (taken as a whole). The proportions obtained were then plotted against time (hereafter termed proportion curves). In analysing these proportions, it is important to recall that the 'invasion curve' of native species represents the history of the state of knowledge of the range occupied by these species. The range is not really expanding over time: it is simply better known. Consequently, if the proportion (of exotic vs. native species) is increasing for a particular time period, this strongly suggests that the area occupied by the exotic species is really expanding, because it is expanding faster than if it was strictly the result of better spatial coverage of the sampling for herbarium specimens. If the proportion remains stable, the area occupied by the exotic species may be expanding; however, this expansion could simply be related to better spatial coverage of the sampling effort. Neither hypothesis can be rejected. If the proportion is declining, the area occupied by the exotic species may still be expanding, but at a very slow rate: although the knowledge of the spatial distribution of plant species is improving, additional 10×10-km^2 occupied by the exotic species are rarely found.

RESULTS

Native species

A total of 5557 herbarium specimens (native species: 2889; exotic species: 2668) were used in this study. During the last 200 years, the degree of sampling for herbarium specimens of native wetland plants was highly variable (Fig. 2). The first specimens were collected in 1820, but very few specimens were collected before 1925. During the twentieth century, two periods of intensive collection can be clearly distinguished, i.e. from 1930 to 1940 and from 1950 to 1985. From 1985 onwards, the collection of herbarium specimens decreased strongly to return to nineteenth century levels between 1995 and 2000.

The spatial distribution of the herbarium specimens of three of the five native species is shown in Fig. 3. Before 1925, most herbarium specimens were sampled along the St Lawrence River, mainly near the largest cities, Montréal and Québec City. The spatial distribution of herbarium records covered most of the St Lawrence River, from Montréal to the Îles-de-la-Madeleine. From 1925 onwards, a large number of additional herbarium specimens were recorded, but the species distribution did not expand much in any direction (except *L. terrestris* in the northwest), suggesting a stable distribution during the twentieth century. The invasion curve of all native species (taken as a whole) has a sigmoidal shape (Fig. 2). Before 1890, the increase in new 10×10-km^2 was slow. The increase was fairly constant from 1890 to 1990, and then reached a plateau from 1990 onwards.

Exotic species

The historical pattern of the sampling effort for exotic plants is similar to that for native species (Fig. 4). Few herbarium specimens were collected either during the nineteenth century or since 1990. Most exotic specimens were collected *c.* 1925–35 (except for species introduced after 1950), and especially between 1960 and 1985. *Lythrum salicaria* was collected far more frequently than the other five exotic species. *Lythrum salicaria* was first collected in 1883 (Québec City) and 1890 (Montréal). No herbarium specimen

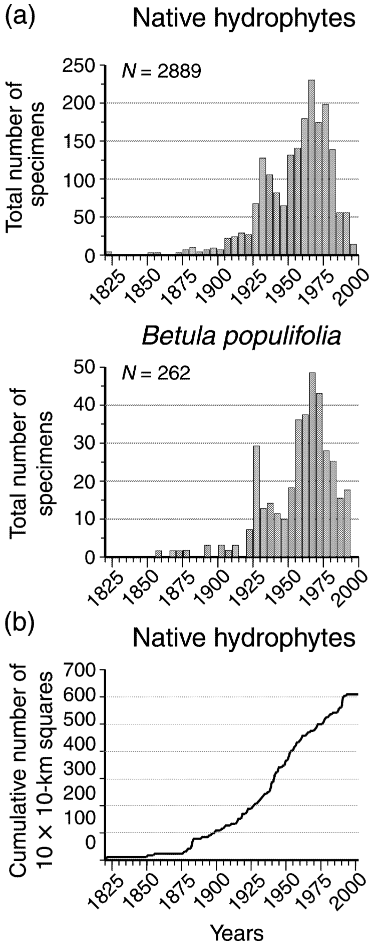

Figure 2 Total number of herbarium specimens collected in Québec per 5-year period for five native vascular plants found in wetlands (all species considered), and for grey birch [*Betula populifolia* (Marsh.)] (a). Data on grey birch are from Lavoie & Saint-Louis (1999). Invasion curve (sensu Pyšek & Prach, 1993) of five native vascular plants found in wetlands of Québec (b). Results are expressed as the cumulative number of $10 \times 10\text{-km}^2$ occupied by at least one of the five species over time. For native species, 'invasion curve' indicates the spatiotemporal distribution of the sampling for herbarium specimens of wetland plants. It also represents the history of the state of knowledge of the distribution of native species.

of *L. salicaria* was collected along roadsides before 1940. During the last 60 years, the proportion of herbarium specimens collected along roadsides increased from 2–9% (1941–80) to 23–25% (1981–2000). The slope of the invasion curve of this species is abrupt and differs significantly ($P < 0.01$) from that of the native species (Fig. 5a). Two major periods of invasiveness can be distinguished in the proportion curve, i.e. from 1890 to 1905 and from 1923 to 1946, respectively (Fig. 5b). During the last 50 years, the spatial distribution of this species did not expand much (Fig. 5c).

The first herbarium specimens of *P. australis* were collected in 1820 near Montréal and Québec City. However, few specimens were collected before 1925. Very few specimens were collected along roadsides before 1969. From 1969 onwards, 37% of all specimens were collected near roadsides. The slope of the invasion curve of this species does not differ significantly ($P > 0.5$) from that of the native species (Fig. 5a). Nevertheless, one period of invasiveness is apparent in the proportion curve from 1963 to 1984 (Fig. 5b). A large number of *P. australis* specimens were collected in Québec in 1985 (Fig. 4) to study chromosome numbers and reproductive aspects of several populations (Gervais *et al.*, 1993). This collection explains the abrupt rise in the proportion curve that year (Fig. 5b).

Butomus umbellatus was discovered in 1905 near Montréal and was present near Québec City as early as 1922. The slope of the invasion curve of this species is abrupt and significantly different ($P < 0.01$) from that of the native species (Fig. 5a). One major period of invasiveness can be delineated in the proportion curve from 1922 to 1935 (Fig. 5b). During the last 50 years, the spatial distribution of this species did not expand much, although some colonies became established in the Gaspé Peninsula and in the Lake St Jean area (Fig. 5c).

Rorippa amphibia was discovered in 1927 near Lake St Pierre. The slope of the invasion curve of this species does not differ significantly ($P > 0.5$) from that of the native species (Fig. 5a). However, if we compare the invasion curves for only the period when *R. amphibia* was present in the study area (1927–2000), there is a significant difference ($P < 0.01$). Three periods of invasiveness are noticeable in the proportion curve, i.e. from 1929 to 1934, from 1943 to 1952, and from 1971 to 1979, respectively (Fig. 5b). The range of this species is almost exclusively restricted to the course of the St Lawrence River (Fig. 5c).

The two other exotic species (*H. morsus-ranae* and *L. europaeus*) were introduced later (1952–63) and have very abrupt invasion curves that differ significantly ($P < 0.01$) from that of the native species (Fig. 5a). The range of these species was still expanding in the 1990s (Fig. 5b) and both had a very similar invasion pattern, almost exclusively restricted to the course of the St Lawrence River (Fig. 5c). Maximum rates of spread along the St Lawrence River ranged from 15 km year^{-1} for *H. morsus-ranae* (1957–74, i.e. from Montréal to Québec City) to 45 km year^{-1} for *L. europaeus* (1963–74, i.e. from Montréal to Trois-Pistoles), respectively.

DISCUSSION

Historical reconstruction of the degree of sampling for herbarium specimens

The degree of sampling for herbarium specimens in Québec was not constant over time, even during the twentieth century. This variable sampling effort is brought to the fore by the historical reconstruction of the sampling of native wetland species. This sampling history is very similar to that of grey birch (*Betula populifolia* Marsh.) specimens (Fig. 2) mainly collected in old fields in Québec

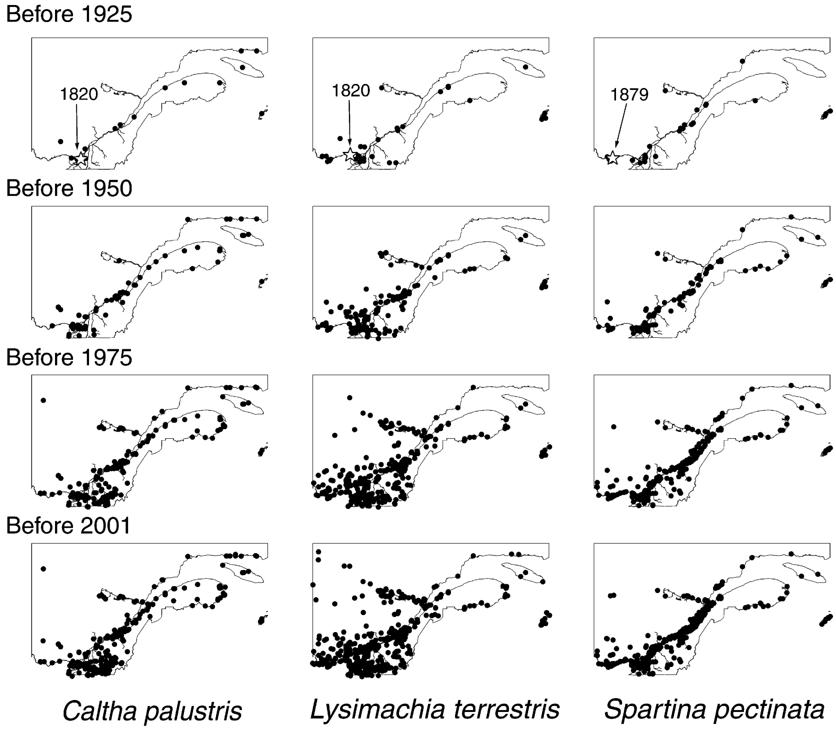

Figure 3 Location of herbarium specimens (black dots) of three native vascular plants found in wetlands of Québec and collected before 1925, 1950, 1975 and 2001, respectively (b). The year and location (white star) of the oldest herbarium specimen are indicated.

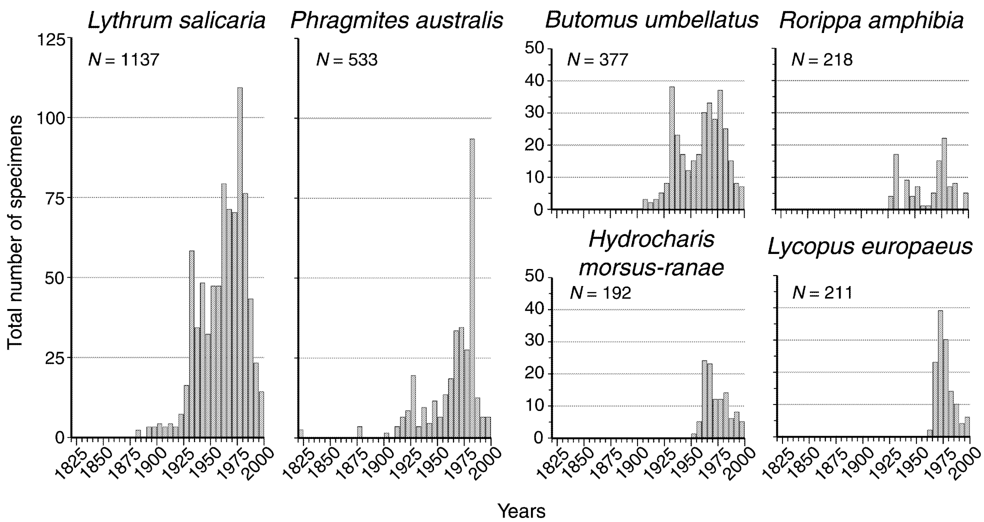

Figure 4 Total number of herbarium specimens collected in Québec per 5-year period for six exotic vascular plants found in wetlands.

(Lavoie & Saint-Louis, 1999), suggesting that it is representative of the global sampling effort in the province. The loss (fire) of some nineteenth century collections and the low number of botanists in Québec before 1920 (Boivin, 1980; Chartrand *et al.*, 1987) are problematical for reconstructing the spread of invasive species introduced more than 80–100 years ago. During the 1930s, several botanists were very active in Québec, in particular Frère Marie-Victorin, Père Louis-Marie and their students. The large number of herbarium specimens sampled during this decade facilitates historical phytogeographical studies. The death of Frère Marie-Victorin in 1944 and economic problems in the 1940s arising from fuel rationing during the Second World War contributed to reducing the number of botanical surveys (Rumilly, 1949; Chartrand *et al.*, 1987). A new generation of botanists (namely B. Boivin, J. Cayouette, L. Cinq-Mars, E. Lepage, E. Rouleau, C. Rousseau, J. Rousseau and H.J. Scoggan, among others) were very active in Québec from 1950 to 1985, and historical reconstruction of the spread of invasive species may

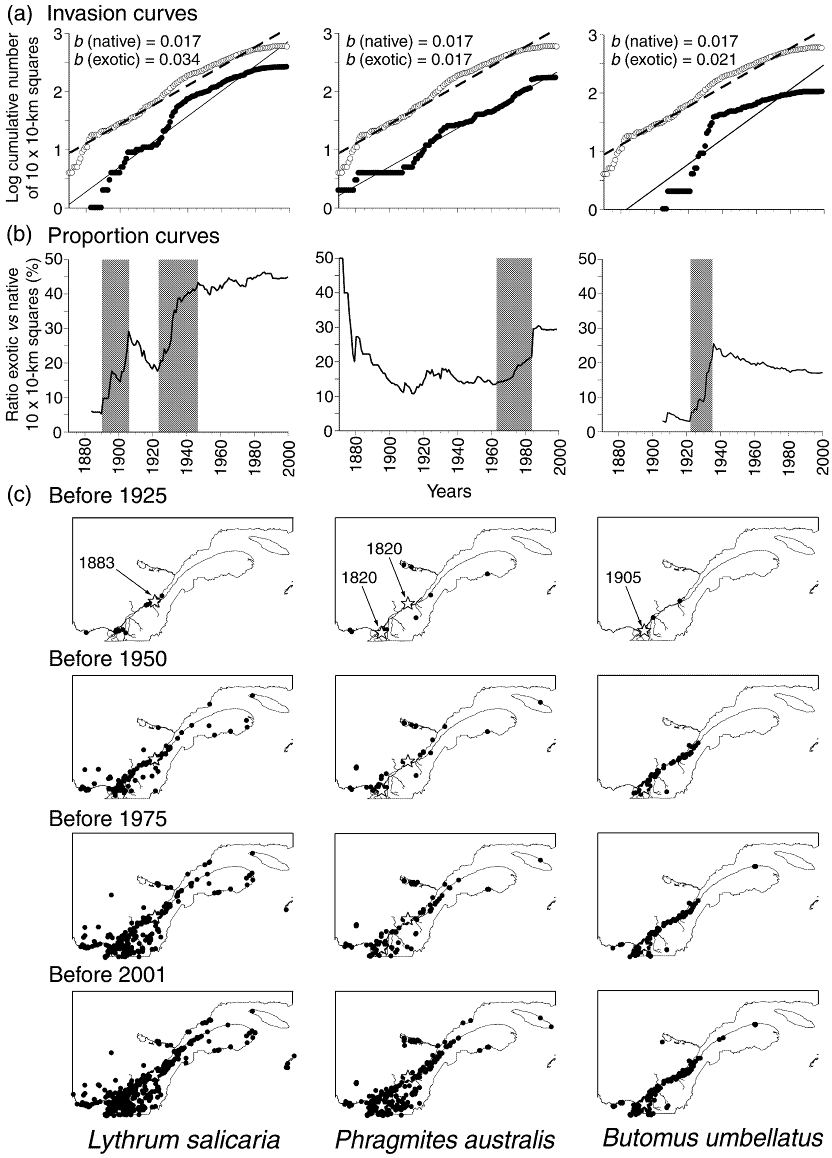

Figure 5 Invasion curves of six exotic vascular plants (solid lines and closed circles) compared with the invasion curve of five native vascular plants taken as a whole (dotted lines and open circles) (a). All species are found in the wetlands of Québec. Results are expressed as the logarithm of the cumulative number of $10 \times 10\text{-km}^2$ occupied by the species over time. The rare herbarium specimens that were collected before 1870 were not considered. Invasion rate (slope b of the regression equation) is given for each exotic species and for the group of native species. Proportion curves (cumulative number of $10 \times 10\text{-km}^2$ for each exotic species divided by that for native species taken as a whole) calculated for each year on record for the six exotic vascular plants (b). Periods of invasiveness are indicated by grey zones (see Methods for details). Location of herbarium specimens (black dots) of the same exotic species collected in Québec before 1925, 1950, 1975 and 2001, respectively (c). The year and location (white star) of the oldest herbarium specimen are indicated.

be more accurate during these decades. After 1985, the interest in traditional floristic studies declined, and a shift occurred from taxonomic to ecological studies, thereby reducing the number of herbarium specimens being collected. In summary, the highly variable sampling effort in Québec and in other regions (MacDougall *et al.*, 1998; Hedenäs *et al.*, 2002) strongly cautions against using herbarium data without correction procedures.

Proportion curves

The method used to take into account the biases associated with the variable sampling for herbarium specimens (construction of proportion curves) is very simple and reliable for objectively delineating periods of invasiveness for exotic species. We cannot totally exclude the possibility that exotic species were invasive during other periods, but the use of proportion curves (exotic vs. native species) helps biogeographers to identify periods during which the phenomenon was particularly obvious. Invasion rates calculated using invasion curves (*sensu* Pyšek & Prach, 1993) could also be useful to compare one exotic species to another, but in Québec, calculated rates are probably strongly influenced by the intensity of floristic research during a particular time period. For instance, the spread of *H. morsus-ranae* and *L. europaeus* coincided with a period of intensive herbarium specimen collection in Québec. The reconstruction of the initial phase of the invasion pattern is probably more accurate for these species than for *L. salicaria* and *B. umbellatus*, which were introduced much earlier. This

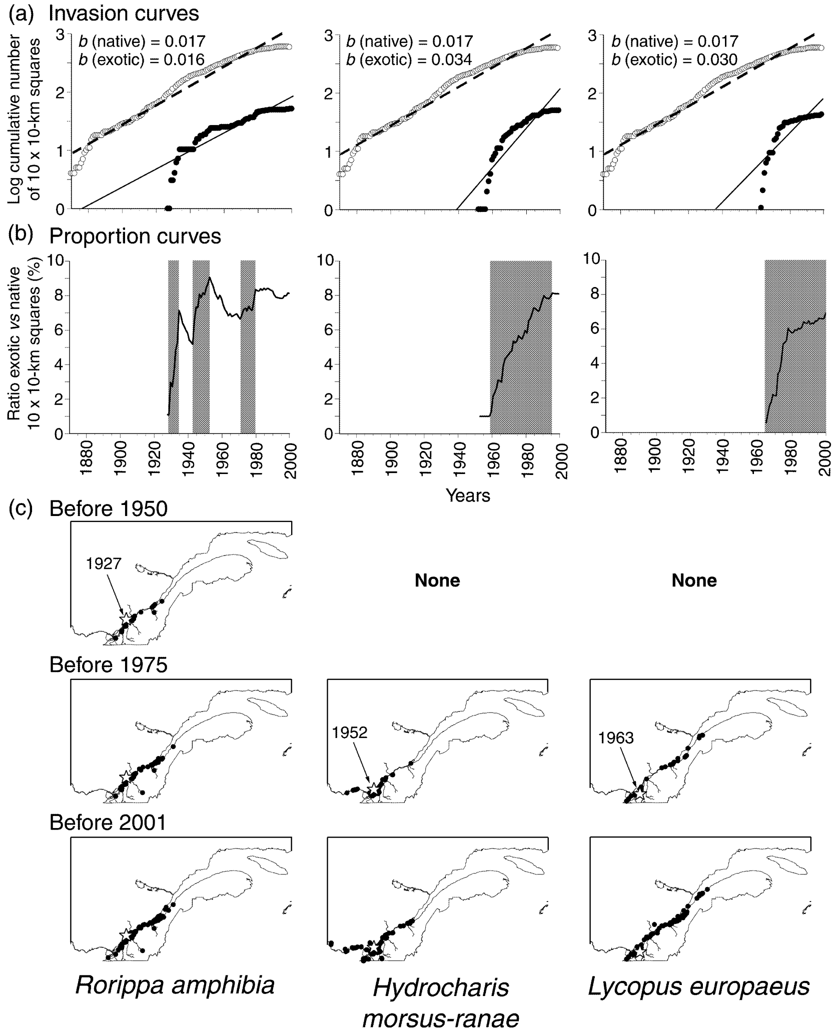

Figure 5 *continued*

may explain why no lag was observed between the discovery of the first specimen of *H. morsus-ranae* and *L. europaeus* and the beginning of the expansion phase, during which populations increase spatially (Lambrinos, 2001). Furthermore, the saturation phase, during which the invasion rate slows down because biotic and abiotic barriers are encountered (Lambrinos, 2001), has apparently not yet been reached for the recently introduced *H. morsus-ranae* and *L. europaeus*. The lack of a saturation phase contributes to increase the calculated invasion rates.

Patterns and causes of spread of exotic species

Using the information provided by proportion curves and distribution maps of herbarium specimens, we can examine the invasion patterns and suggest some causes to explain the rapid spread of exotic species. Most species appear to use the St Lawrence River as a major dispersal vector. Exotic wetland species rapidly established colonies along the fluvial section (from Montréal to Lake St Pierre) and the freshwater estuary (from Lake St Pierre to Québec City), and then populations expanded locally. For instance, *B. umbellatus* required less than 17 years (1905–22) to establish scattered colonies between Montréal and Québec City (founding phase of Lambrinos, 2001). The establishment of colonies has certainly been facilitated by the fact that *B. umbellatus* has rhizome fragments or bulbils that are easily dispersed by water (Hroudová *et al.*, 1996). Furthermore, populations of *B. umbellatus* located in eastern Canada exhibit a high level of sexual fertility, and the seeds they produce are also highly viable. As seeds may disperse over longer distances than vegetative fragments (Eckert *et al.*, 2000), these characteristics may further increase the rate at which this species spreads. The expansion phase, during which populations increase spatially, was very short, and occurred between 1922 and 1935 (mainly in the 1930s), according to the proportion curve of this species. The rapid spread of *B. umbellatus* during the 1930s is probably associated with low water levels in the St Lawrence River: several emergent marshes were invaded by this species, particularly in the Montréal area (Marie-Victorin, 1943). The warmer temperatures of newly exposed soils promote sprouting of *B. umbellatus*, which leads to multiplication of shoots and establishment of new individuals from rhizome fragments (Hroudová *et al.*, 1996). After 1935, the saturation phase was apparently reached: most freshwater marshes of the St Lawrence River were already invaded. Downstream from Québec City, the salinity of surface waters of the St Lawrence River probably prevented the establishment of colonies of *B. umbellatus*, as with many other plant species (Lachance & Lavoie, 2002; Lavoie *et al.*, 2003).

The invasion patterns of *R. amphibia*, *H. morsus-ranae* and *L. europaeus* are very similar to that of *B. umbellatus* from a spatial point of view. No founding phase was found, but, as indicated above, this may be a consequence of the increased sampling effort after 1925. There is little information about the biology of *R. amphibia*, and we were not able to associate the three expansion phases with water level fluctuations or any other kinds of disturbance. The rapid spread of *H. morsus-ranae* along the St Lawrence River can be explained by the numerous overwintering buds (turions) that are produced each year and dispersed by water in spring (Scribailo & Posluszny, 1984). Likewise, the exceptionally rapid expansion of *L. europaeus* can be explained by the fact that seeds remain viable after floating for 12–15 months (Stuckey, 1969). Although the proportion curves of *H. morsus-ranae* and *L. europaeus* suggest that the range of these species is still expanding, it will probably not expand north-eastward along the St Lawrence River because of the salinity of surface waters and the scarcity of large riverine wetlands east of Trois-Pistoles (Catling & Porebski, 1995; Lachance & Lavoie, 2002). Nevertheless, Delisle (2002) found a *H. morsus-ranae* population in 2001 in a freshwater drainage ditch at St Roch-des-Aulnaies (Fig. 1), which represents a major (93 km) north-eastward expansion of the range of this species in Québec.

Although the first herbarium specimen of *L. salicaria* was not collected in Québec before 1883, there is evidence that the species was present in north-eastern North America long before that date. *L. salicaria* is mentioned in Pursh's (1814) *Flora Americae Septentrionalis*. Seeds of *L. salicaria* were sold in Québec, Massachusetts, New York and Ohio nurseries as early as 1829 (Guibault, 1834; Mack, 1991). The earliest known herbarium specimens in North America were collected in Massachusetts in 1831 (Stuckey, 1980). In Québec, the species was found near Québec City *c.* 1865 (Brunet, 1865). Consequently, and considering the high fertility level of *L. salicaria* and the fact that seeds are easily dispersed by water (Thompson *et al.*, 1987), it is more likely that the expansion phase began in Québec before 1890, i.e. before the first major rise in the proportion curve of *L. salicaria*. It is difficult to track the expansion phase of *L. salicaria* using herbarium records because very few specimens were collected in the nineteenth century.

The spread of *L. salicaria* and of *P. australis* has not been restricted to the course of the St Lawrence River, especially in the south-western part of Québec. Both species produce large amounts of seeds that are easily dispersed by water or wind over long distances (Haslam, 1972; Thompson *et al.*, 1987; Gervais *et al.*, 1993). Furthermore, the spread of *L. salicaria* was probably accelerated by numerous introductions for ornamental purposes (Thompson *et al.*, 1987). Roads probably contributed to the spread of this species (Wilcox, 1989). However, this contribution seems to have only occurred during the last 20 years in Québec. Furthermore, the spread of *P. australis* from 1963 to 1984 was probably associated with the expansion of the highway system in southern Québec. Almost all highways in Québec were built between 1963 and 1983, especially between 1964 and 1968 (Ministère des Transports du Québec, 1983). Mechanical digging of road ditches favours the spread of this species by fragmenting rhizomes and displacing them over large distances (Gervais *et al.*, 1993).

CONCLUSION

Numerous biases complicate the use of herbarium specimens for the historical reconstruction of biological invasions. However, the variability of the sampling effort over time can be taken into account by comparing invasion curves of exotic species with those of native species, and by constructing proportion curves. Proportion curves allow the objective delineation of periods of invasiveness for exotic species. The method proposed in this paper is quite simple using a geographical information system. However, it is more appropriate for species that are regularly collected (at least one herbarium specimen per year) and that occupy large areas. For instance, the 10 × 10-km grid is too large to track the invasion pattern of species that have been introduced very recently and/or are restricted to a small area (Delisle, 2002). Furthermore, this method requires not only a good knowledge of the history of herbarium specimen collection, but also of the native flora, which is used as a control.

The spread of wetland vascular plant species can be reconstructed using herbarium specimens, even when the phenomenon is rapid, but this reconstruction is certainly more accurate when the invasion occurs during an active collection period. The recent lack of interest in both floristic research and sampling for herbarium specimens in Québec and in other parts of the world (MacDougall *et al.*, 1998; Hedenäs *et al.*, 2002) is worrisome: major gaps in data will seriously hamper future historical reconstructions of biological invasions, and consequently will complicate the understanding and modelling of such processes.

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REFERENCES

Boivin, B. (1980) Survey of Canadian herbaria. *Provancheria*, **10**, 1–187.

Brunet, O. (1865) *Catalogue des plantes canadiennes contenues dans l'herbier de l'Université Laval et recueillies pendant les années 1858–65*. C. Darveau, Québec, p. 38.

Catling, P.M. & Porebski, Z.S. (1995) The spread and current distribution of European frogbit, *Hydrocharis morsus-ranae* L., in North America. *Canadian Field-Naturalist*, **109**, 236–241.

Chambers, R.M., Meyerson, L.A. & Saltonstall, K. (1999) Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic Botany*, **64**, 261–273.

Chartrand, L., Duchesne, R. & Gingras, Y. (1987) *Histoire des sciences au Québec*. Boréal, Montréal, p. 487.

Delisle, F. (2002) *L'utilisation des spécimens d'herbier dans la reconstitution historique des invasions biologiques des milieux humides du fleuve Saint-Laurent*. Unpublished M.ATDR Thesis, Université Laval, Sainte-Foy, p. 37.

Eckert, C.G., Massonnet, B. & Thomas, J.J. (2000) Variation in sexual and clonal reproduction among introduced populations of flowering rush, *Butomus umbellatus* (Butomaceae). *Canadian Journal of Botany*, **78**, 437–446.

Gervais, C., Trahan, R., Moreno, D. & Drolet, A.-M. (1993) Le *Phragmites australis* au Québec: distribution géographique, nombres chromosomiques et reproduction. *Canadian Journal of Botany*, **71**, 1386–1393.

Guibault, S. (1834) *Catalogue of fruit and ornamental trees, flowering shrubs and plants, green-house shrubs and plants, bulbous flower roots, American and indigenous trees and plants, flower and garden seeds, cultivated and for sale at Guibault Botanic Garden, Coteau-Baron, St Lawrence Street, Montreal*. Ludger Duvernay, Montréal, p. 40.

Harris, R.J. (1975) *A Primer of Multivariate Statistics*. Academic Press, New York, p. 332.

Haslam, S.M. (1972) Biological flora of the British Isles: *Phragmites communis* Trin. *Journal of Ecology*, **60**, 585–610.

Hedenäs, L., Bisang, I., Tehler, A., Hamnede, M., Jaederfelt, K. & Odelvik, G. (2002) A herbarium-based method for estimates of temporal frequency changes: mosses in Sweden. *Biological Conservation*, **105**, 321–331.

Hroudová, Z., Krahulcová, A., Zákravský, P. & Jarolímová, V. (1996) The biology of *Butomus umbellatus* in shallow waters with fluctuating water level. *Hydrobiologia*, **340**, 27–30.

Johansson, M.E., Nilsson, C. & Nilsson, E. (1996) Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*, **7**, 593–598.

Lachance, D. & Lavoie, C. (2002) Reconstructing the biological invasion of European water-horehound, *Lycopus europaeus* (Labiatae), along the St Lawrence River, Québec. *Rhodora*, **104**, 151–160.

Lambrinos, J.G. (2001) The expansion history of a sexual and asexual species of *Cortaderia* in California, USA. *Journal of Ecology*, **89**, 88–98.

Lavoie, C. & Saint-Louis, A. (1999) The spread of gray birch (*Betula populifolia*) in eastern Quebec: landscape and historical considerations. *Canadian Journal of Botany*, **77**, 859–868.

Lavoie, C., Jean, M., Delisle, F. & Létourneau, G. (2003) Exotic plant species of the St Lawrence River wetlands: a spatial and historical analysis. *Journal of Biogeography*, **30**, 537–549.

Lonsdale, W.M. (1993) Rates of spread of an invading species: *Mimosa pigra* in northern Australia. *Journal of Ecology*, **81**, 513–521.

MacDougall, A.S., Loo, J.A., Clayden, S.R., Goltz, J.G. & Hinds, H.R. (1998) Defining conservation priorities for plant taxa in southeastern New Brunswick, Canada using herbarium records. *Biological Conservation*, **86**, 325–338.

Mack, R.N. (1991) The commercial seed trade: an early disperser of weeds in the United States. *Economic Botany*, **45**, 257–273.

MapInfo Corporation (2001) *MapInfo Professional*. Version 6.5. Troy.

Marie-Victorin, F. (1943) Observations botaniques sur les effets d'une exceptionnelle baisse de niveau du Saint-Laurent durant l'été de 1931. *Contributions de l'Institut botanique de l'Université de Montréal*, **48**, 21–28.

Mihulka, S. & Pyšek, P. (2001) Invasion history of *Oenothera* congeners in Europe: a comparative study of spreading rates in the last 200 years. *Journal of Biogeography*, **28**, 597–609.

Ministère des Transports du Québec (1983) *Les autoroutes du Québec: dates de construction ou de mise en service*. Gouvernement du Québec, Québec, p. 31.

Pursh, F. (1814) *Flora Americae Septentrionalis*. White, Cochrane & Co., London, p. 751.

Pyšek, P. (1991) *Heracleum mantegazzianum* in the Czech Republic: dynamics of spreading from the historical perspective. *Folia Geobotanica et Phytotaxonomica*, **26**, 439–454.

Pyšek, P. & Prach, K. (1993) Plant invasion and the role of riparian habitats: a comparison of four species alien to central Europe. *Journal of Biogeography*, **20**, 413–420.

Pyšek, P. & Prach, K. (1995) Invasion dynamics of *Impatiens glandilufera*: a century of spreading reconstructed. *Biological Conservation*, **74**, 41–48.

Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.

Reznicek, A.A. & Catling, P.M. (1987) *Carex praegracilis* (Cyperaceae) in eastern North America: a remarkable case of rapid invasion. *Rhodora*, **89**, 205–216.

Rich, T.C.G. & Smith, P.A. (1996) Botanical recording, distribution maps and species frequency. *Watsonia*, **21**, 155–167.

Rich, T.C.G. & Woodruff, E.R. (1992) Recording bias in botanical surveys. *Watsonia*, **19**, 73–95.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.

Rumilly, R. (1949) *Le frère Marie-Victorin et son temps*. Frères des Écoles chrétiennes, Montréal, p. 459.

Saltonstall, K. (2002) Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences*, **99**, 2445–2449.

Scribailo, R.W. & Posluszny, U. (1984) The reproductive biology of *Hydrocharis morsus-ranae*. I. Floral biology. *Canadian Journal of Botany*, **62**, 2779–2787.

Stuckey, R.L. (1969) The introduction and spread of *Lycopus asper* (western water-horehound) in the western Lake Erie and Lake St Clair region. *Michigan Botany*, **8**, 111–120.

Stuckey, R.L. (1980) Distributional history of *Lythrum salicaria* (purple loosestrife) in North America. *Bartonia*, **47**, 3–20.

Thompson, D.Q., Stuckey, R.L. & Thompson, E.B. (1987) *Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands*. US Fish and Wildlife Service, Washington, DC, p. 55.

Urmi, E. & Schnyder, N. (2000) Bias in taxon frequency estimates with special reference to rare bryophytes in Switzerland. *Lindbergia*, **25**, 89–100.

Weber, E. (1998) The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography*, **25**, 147–154.

White, D.J., Haber, E. & Keddy, C. (1993) *Plantes envahissantes des habitats naturels du Canada*. Environnement Canada and Musée canadien de la nature, Ottawa, p. 136.

Wilcox, D.A. (1989) Migration and control of purple loosestrife (*Lythrum salicaria* L.) along highway corridors. *Environmental Management*, **13**, 365–370.

Zar, J.H. (1996) *Biostatistical analysis*, 3rd edn. Prentice Hall, Upper Saddle River, p. 662.

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