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Effect of the invasive common reed on the abundance, richness and diversity of birds in freshwater marshes

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Abstract

The Eurasian genotype of common reed *Phragmites australis* subsp. *australis* is rapidly invading freshwater marshes in North America. Several bird species depend upon particular plant assemblages for feeding and reproduction and could be adversely affected by the expansion of this invader. The objective of this study was to evaluate the effect of common reed on the abundance, richness, diversity and site occupancy of bird assemblages in freshwater marshes recently invaded by the plant (southern Quebec, Canada). We conducted fixed-distance point counts for songbirds (passerines and rails) and visual surveys for waterbirds (ducks, geese and waders) during two nesting seasons (2009 and 2010). There were major structural differences between common reed stands and marsh vegetation assemblages dominated by other plant species (bulrushes, cattails, sedges). However, there was a little difference in abundance, richness, diversity and site occupancy for songbirds. Marsh wren *Cistothorus palustris*, a wetland specialist, was the only nesting bird that preferred a native plant (cattail) over common reed, probably because common reed stands have low plant diversity and few appropriate nest materials. No major differences were observed in the abundance of waterbirds between invaded and non-invaded marshes. For most bird species, the water depth of the marsh had more influence on the abundance of individuals and on site occupancy than the composition of the plant assemblage. Common reed stands can therefore be used by generalist and specialist marsh passerines as feeding and reproduction sites. However, it is possible that in southern Quebec, the number and extent of common reed populations have not yet reached a threshold beyond which adverse effects of the invader on avian species could be significant. This study adds to a growing body of evidence showing that the relationship between invasive plants and birds is not straightforward.

Introduction

Wetlands are strongly disturbed by biological invasions: though they cover only 6% of the surface of the Earth, they host 24% of the most invasive species on the planet (Zedler & Kercher, 2004). Several bird species depend upon specific marsh plant assemblages for feeding and reproduction (Weller, 1994; Gjerdrum, Elphick & Rubega, 2005) and can be adversely affected by the expansion of plant invaders. They can lose the native vegetation types that are preferably used as nesting sites or as refuges from predators (Johnson & Dinsmore, 1986; Lor & Malecki, 2006). They can also lose invertebrate-rich feeding habitats, such as the interfaces between vegetation stands and open water areas (Kaminski & Prince, 1981; Rehm & Baldassarre, 2007), once the areas without plant cover are occupied by the invaders. Finally, their mobility can be restricted by the biomass produced by productive plant invaders. For example, waterfowl foraging can be hampered by floating or submerged plants forming a dense and thick carpet near the water surface (Ma *et al*., 2010).

As recently highlighted by Schlossberg & King (2010), research on the effects of invasive plants on avian species have produced equivocal results. In wetlands, plant species like smooth cordgrass *Spartina alterniflora* and common water hyacinth *Eichhornia crassipes* had significant negative impacts on the abundance of marsh birds (Gan *et al*., 2009; Gunaratne, Jayakody & Bambaradeniya, 2009). In contrast, other invasive species such as purple loosestrife *Lythrum salicaria* and waterthyme *Hydrilla verticillata* apparently have little effects on birds (Hoyer *et al*., 2008; Lavoie, 2010). In North America, marsh birds are increasingly exposed to the exotic subspecies of the common reed *Phragmites australis* subsp. *australis* that is rapidly spreading through freshwater wetlands (Guo *et al*., 2013), especially around the Great Lakes (Wilcox *et al*., 2003; Trebitz & Taylor, 2007; Tulbure, Johnston & Auger, 2007; Whyte *et al*., 2008; Tulbure & Johnston, 2010; Wilcox, 2012) and along the St. Lawrence River (Hudon, Gagnon & Jean, 2005). Once established in a marsh, common reed quickly forms large, homogeneous populations with low plant diversity (Ailstock, Norman & Bushmann, 2001; Lavoie *et al*., 2003). This grass species also accumulates litter at a much higher rate than that of the majority of native plants, which contributes to a gradual filling of the marsh bed (Windham & Lathrop, 1999; Meyerson *et al*., 2000).

In freshwater marshes, the few studies that examined the effects of common reed on fishes (Aday, 2007; Kulesza, Holomuzki & Klarer, 2008; Larochelle, 2011), turtles (Bolton & Brooks, 2010), amphibians (Meyer, 2003; Perez, 2011) and mammals (Meyer, 2003; McGlynn, 2006) revealed low to moderate effects on animal populations. Information on the effect of common reed on birds remains limited and sometimes contradictory. In the freshwater and brackishwater marshes of New York, avian diversity was reduced by common reed: red-winged blackbird *Agelaius phoeniceus*, a generalist species, took advantage of the presence of the invader for perching and roosting, but other wetland-specialist birds like the least bittern *Ixobrychus exilis*, marsh wren *Cistothorus palustris* and Virginia rail *Rallus limicola* had a reduced number of nests in invaded sites (Wells *et al*., 2008). In brackishwater marshes of Connecticut, some wetland-specialist birds (marsh wren, swamp sparrow *Melospiza georgiana*) benefited from the presence of common reed, while other marsh-nesting birds (saltmarsh sparrow *Ammodramus caudacutus*, seaside sparrow *Ammodramus maritimus*) were less abundant in common reed stands than in short-grass assemblages of native plants (Benoit & Askins, 1999). The same phenomenon (a combination of winners and losers) was also observed in Ontario (Meyer *et al*., 2010) and Virginia (Paxton, 2007). To date, common reed does not apparently have large effects on bird richness and abundance in freshwater marshes (McGlynn, 2006; Meyer *et al*., 2010), but to what extent this situation may be changing with the spread of the invader remains unknown. For instance, although only 200 ha of riverine marshes are currently (2010) invaded by common reed along the St. Lawrence River, climate change and ecohydrological models predict that the area occupied by the plant could increase to 17 000 ha in the near future (Tougas-Tellier, 2013). Wetland bird assemblages will likely be affected by such a large invasion.

The main objective of this study was to evaluate the effect of common reed invasions on bird assemblages in freshwater marshes of southern Quebec (Canada), where the plant is currently rapidly expanding its range (Hudon *et al*., 2005; Lelong *et al*., 2007). We determined whether the invader already had some impacts on the abundance, richness, diversity and site occupancy of birds. We targeted four groups of birds which represent the majority of species using marshes during the spring/summer [i.e. the Passeriformes (passerines), Rallidae (rails), Anatidae (ducks and geese) and Ardeidae (waders)]. We predicted that the passerines that depend exclusively on marshes for food and/or reproduction should be more affected by the invader compared with generalist passerines. We also predicted that the presence and abundance of ducks, geese, rails and waders should be negatively affected by common reed, first because less open water areas are available for feeding and second because common reed hampers their mobility.

Materials and methods

Study area

The study area (Fig. 1) was located in southwestern Quebec where the bulk of common reed populations is found in the province (Jodoin *et al*., 2008). Eight freshwater marshes, five invaded and three not invaded and used as control (or reference) sites, were selected. These marshes were chosen partly because they were invaded to various degrees and partly because they were easily accessible by road and suitable (six of the eight sites) for the establishment of observation towers on dikes. All marshes were located within 1 km of a major river (St. Lawrence River or Ottawa River). The landscape surrounding the marshes was essentially composed by agricultural fields. Four of the five invaded marshes were close to the Beauharnois Canal, three to the south (BC1, BC2 and BC3) and one to the north (BC4) of the canal. These artificial marshes (28–85 ha each), created by Duck Unlimited Canada in 1979, had common reed stands covering 10–35% of their surface. Apart from common reed stands, patches of flowering-rush *Butomus umbellatus* (an exotic species) and cattails *Typha* spp. were also present. The fifth invaded marsh (BV: 86 ha) surrounded some of the islands of the Îles-de-Boucherville National Park near Montreal. This park is currently the most invaded site by common reed along the St. Lawrence River, and the reed stands currently cover 48 ha (Tougas-Tellier, 2013) or about 40% of the sector of the park that has been studied for birds. Stands of cattails and reed canary grass *Phalaris arundinacea* (an exotic species) were also found. Of the eight marshes sampled, it was the only one not surrounded by a dike.

The three non-invaded (control) marshes were man-made impoundments where common reed was absent or confined to the surrounding dikes. The Digue aux Aigrettes marsh (60 ha) was located in the Lac Saint-François National Wildlife Area and dominated by southern wild rice *Zizania aquatica* and a few sedges *Carex* spp. The marsh of the Marguerite-d'Youville Wildlife Refuge (MY: 30 ha), on Saint-Bernard Island, was mostly covered with cattails and arrowheads *Sagittaria* spp. The third marsh, near Thurso (TH: 60 ha), was located in the Plaisance National Park and covered by a highly diversified emergent vegetation including cattails, sedges and southern wild rice. Between 20 and

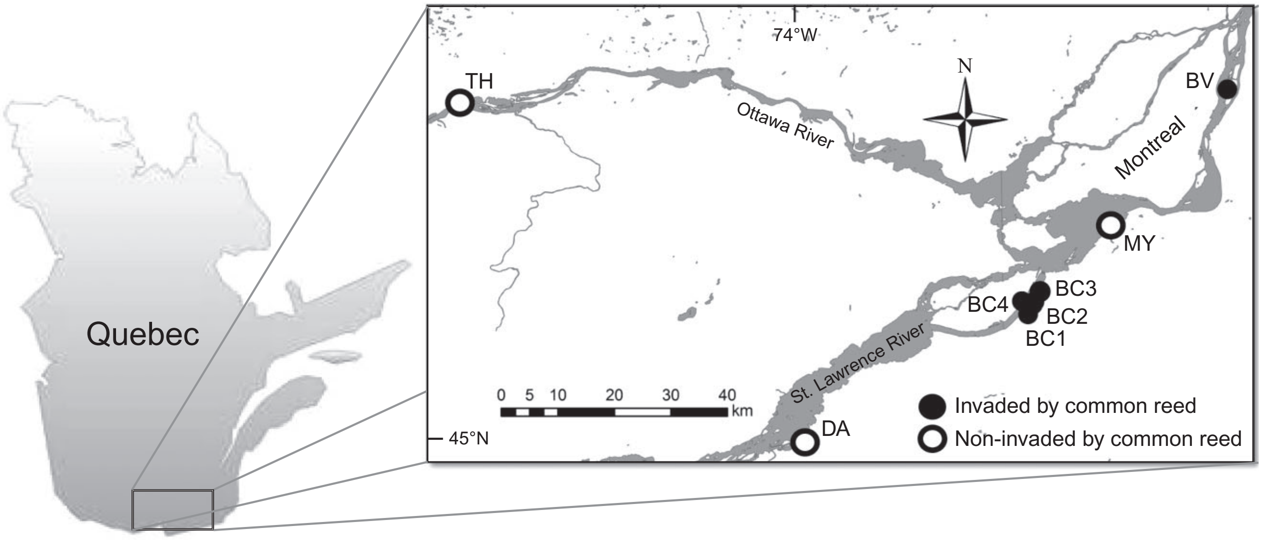

Figure 1 Location of the eight freshwater marshes sampled in 2009 and 2010 in southern Quebec (Canada) to evaluate the effect of invasive common reed *Phragmites australis* on avian species. BC1, BC2, BC3 and BC4, Beauharnois Canal (all invaded); BV, Îles-de-Boucherville National Park (invaded); DA, Digue aux Aigrettes (non-invaded); MY, Marguerite-d'Youville Wildlife Refuge (non-invaded); TH, Thurso (non-invaded).

60% of the area of these marshes were occupied by open water areas (no emergent plant) in mid-July.

Bird surveys

The bird surveys were spread over 2 years (2009 and 2010) from the beginning of May to the end of July during the nesting season. Data were collected in the morning from 5:00 to 10:30 AM on days with light wind and no rain by the same observers each year to ensure consistency in the detection and identification capacities (Boulinier *et al*., 1998). Two methods were used, point counts for songbirds (passerines and rails) and visual counts for waterbirds (ducks, geese and waders). The sampling season was divided into five periods of about 15 days, and each marsh was surveyed once per period to increase chances of bird detection, except for the MY marsh that was visited only once in 2009 due to time constraints.

For locating point counts, a vegetation map was created for each marsh using aerial photographs to circumscribe the main vegetation types, that is (1) common reed stands; (2) cattail stands; (3) the other types of emergent plants dominated by various short forb, grass and sedge species and which were grouped together as 'short-height' vegetation stands. From the vegetation maps, fixed-distance point count stations with a 50-m radius were placed in each of the three vegetation types. Using a geographic information system, each station was positioned ≥50 m from any other vegetation types and ≥250 m from each other to ensure independence of the data (Bird Studies Canada, 2008; Meyer *et al*., 2010). The resulting 36 stations were relocated in the field using a geographic positioning system. In 2009, we surveyed 10 stations in common reed stands, six in cattail stands and 13 in short-height vegetation stands, and in 2010, 15, 8 and 13 stations, respectively. Each of our eight study marshes had between two and seven point count stations, though stations located in common reed stands were obviously restricted to the invaded part of the marshes.

The daily sequence used for visiting the stations at a specific marsh varied between periods because detection probability can diminish with increasing time from sunrise (Lynch, 1995). Listening time at each station was 12 minutes, which is considered as a sufficient amount of time for birds (Ralph, Droege & Sauer, 1995; Dettmers *et al*., 1999). To detect secretive birds, bird calls were broadcasted (4 minutes) during the listening period. The species selected for bird calls were the same as those chosen by Meyer *et al*. (2010), who conducted a similar study in common reed stands in Ontario (i.e. common moorhen *Gallinula chloropus*, least bittern, pied-billed grebe *Podilymbus podiceps*, sora *Porzana carolina* and Virginia rail). Two observers were present during the counts. Every bird detected visually or heard within the station boundaries was identified to the species level. A range finder was used to determine if the bird was within the 50-m radius. For flying birds, only those ≤100 m above the station and which appeared to be hunting were considered (Bird Studies Canada, 2008; Meyer *et al*., 2010).

Visual counts of birds seen in the marshes were made chiefly from 5-m high observation towers. The absence of such structures at BC3 and BV prevented visual counts at these two sites. To cover marsh areas not visible from the towers, observers standing on the dikes simultaneously scanned the marsh and counted the birds. The observers communicated with each other using walkie-talkies to ensure that individuals were not counted twice. Visual counts were made at the same frequency as the point counts. In 2009, 26 visual counts were made (from May 22 to July

24), whereas in 2010, the sampling effort was increased to 29 visits (from May 5 to July 26). Using landmarks on the ground and aerial photographs, the total area under observation from the towers and the dikes was calculated with a geographic information system to adjust the total number of counted individuals observed at each marsh by unit of area (hectare).

Point count station characteristics

The vegetation within each point count station was sampled in July 2010. Five points were sampled per station, one in the center of the station and four others 20 m from the center in the four cardinal directions. At each point, a 2-m rod was laid horizontally on the ground or water surface. A second rod, 4 m long and 3 cm wide with alternating 20-cm red and white bands, was placed upright at one end of the horizontal rod. Each plant species touching the vertical rod was noted, as well as the height of each contact (in 20-cm increments); this operation was repeated each 20 cm along the horizontal rod. Plant species were grouped into the following categories: (1) common reed; (2) sedges or bulrushes; (3) other herbaceous plants (almost exclusively cattails, and hereafter referred as such); (4) other plants (ferns, woody plants, etc.). The total number of contacts per vegetation category and for each height class was calculated for the five sampling points. The average number of contacts per station was then calculated for point count stations dominated by common reed, cattails and short-height vegetation. This method was also used to estimate the percentage of a station occupied by open water (here, inundated sites with no emergent vegetation). Finally, at each visit, the water depth at the center of each station was measured; a zero value was attributed to a water level below the soil surface.

Statistical analyses

Because point count stations were visited more than once, we used site occupancy models to determine the occupancy probability. These models take into consideration the fact that an undetected individual was not necessarily absent from the study site and allow a separate estimate of the probability of occurrence (ψ) and of detection (p) of a species, which may vary by site (MacKenzie *et al.*, 2006). Brown-headed cowbird *Molothrus ater*, common grackle *Quiscalus quiscula*, common starling *Sturnus vulgaris* and red-winged blackbird were excluded from the site occupancy analyses as they were present at almost all the stations. The first bird assemblage considered for analyses grouped the generalist passerines (i.e. birds that use marshes during their life cycle but that do not exclusively depend on it) according to the Canadian Wildlife Service, Ontario Region (2006). This group included song sparrow *Melospiza melodia* (reference species), American goldfinch *Spinus tristi*, American yellow warbler *Setophaga aestiva*, chipping sparrow *Spizella passerina* and willow flycatcher *Empidonax traillii*. Specialist passerines – birds nesting in marshes – formed the second assemblage. This group included swamp sparrow (reference species), common yellowthroat (*Geothlypis trichas*) and marsh wren. Rails formed a third assemblage and included Virginia rail (reference species), common moorhen and sora.

For each bird assemblage, we examined the effects of habitat variables associated with point count stations on the site occupancy probability. The variables were (1) the vegetation type, that is, common reed (reference group), cattail and short-height vegetation; (2) presence of water above the soil surface; (3) the percentage of the station occupied by open water; (4) the average water depth. We considered models where the effect of habitat variables were the same for all the bird species or varied between the species (i.e. with species $\times$ habitat interaction). We also considered the possibility that the detection probability might vary between species. Each model included only one explanatory variable at a time (vegetation or one of the three variables associated with water) to avoid collinearity because preliminary analyses showed significant differences among vegetation types for water-related variables. Ultimately, 31 models capable of explaining the variation in site occupancy probabilities were tested for each bird assemblage. All continuous variables were centered and reduced to normalize their distribution.

The site occupancy analyses were run with programme PRESENCE 3.1 (Patuxent Wildlife Research Center, Patuxent, MD, USA; MacKenzie *et al.*, 2003) for each year separately. Each time, we tested the adjustment of the most general occupancy model (single season) with a bootstrapping procedure (10 000 iterations) to obtain an estimate of c-hat and correct for overdispersion (MacKenzie *et al.*, 2006). We ranked each model based on the second-order Akaike information criterion corrected for overdispersion (QAICc) and calculated the AICc weights to determine the support for each model (Burnham & Anderson, 2002). We calculated the parameter estimates taking into account model selection uncertainty (model averaging) using the AICcMODAVG package of R software (Mazerolle, 2013; R Development Core Team, 2013). The effects of explanatory variables were considered significant when the 95% confidence interval of the slopes (β) excluded 0.

Data for bird abundance, richness and diversity were analysed with mixed linear regression models; we included individual point counts nested within marshes (point count data) or individual marshes (visual count data) as a random effect. The tested variables were as follows: (1) the total abundance (number of individuals per hectare for the particular case of visual counts); (2) the abundance of each species or species assemblage; (3) the richness (total number of species detected); (4) the Shannon diversity index (Magurran, 1988). A log ($x + 1$) transformation was used on these variables to normalize data distribution, except for species abundance data obtained from point counts and for which a generalized mixed model with a Poisson distribution was used.

For point count surveys, we conducted analyses only on species with at least 50 observations during a sampling season. We excluded barn swallows *Hirundo rustica and* tree swallows *Tachycineta bicolor* because their abundance was extremely variable between sampling periods. The five explanatory variables tested in these models were (1) the sampling period; (2) the vegetation type, with common reed still used as the reference group; (3) presence of water above the soil surface; (4) the percentage of the station occupied by open water; (5) the average water depth. Again, each model included only one explanatory variable at a time to avoid collinearity. Eleven models were ultimately compared. Finally, two explanatory variables were tested for visual count surveys (i.e. the sampling period and the presence of common reed in the marsh) for a total of five models. All linear models were adjusted with R software (R Development Core Team, 2013), and model selection and parameter estimation were executed as for site occupancy models.

Results

Vegetation structure

There were major structural differences between the three vegetation types present in point count stations (Fig. 2). The maximal height reached by common reed stems (4.2 m) was much higher than that of cattails (2.4 m) and short-height vegetation (1.2 m). The mean number of contacts per height class also varied greatly among vegetation types. In common reed stands, there were few contacts near the soil/water surface (0–20 cm), and they were most numerous from 20 to 240 cm. In cattail and short-height vegetation stands, most contacts occurred close to the soil/water surface (0–60 cm).

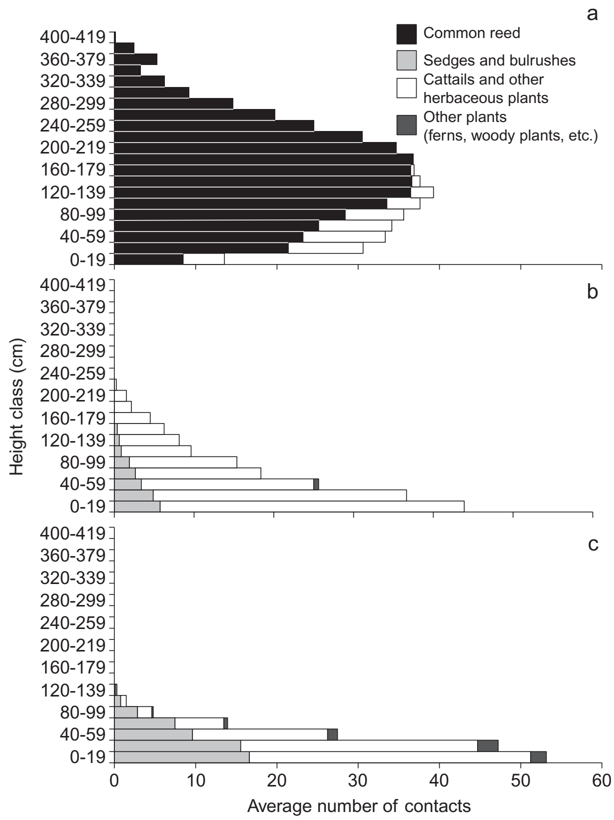

Figure 2 Vegetation structure of the three vegetation types found in the point count stations that were sampled in southern Quebec freshwater marshes for songbird assemblages. Vegetation types were dominated either by (a) common reed *Phragmites australis*, (b) cattails *Typha* spp. or (c) short-height vegetation (various short forb, grass or sedge species). The figure shows the average number of contacts to a vertical rod per height class (20-cm increments) for common reed and three major groups of plants.

Songbirds

In 2009, 1453 bird individuals (excluding swallows) from 48 species were seen or heard during the 109 visits to point count stations. In 2010, 1969 individuals from 47 species were recorded (168 visits). Both years combined, a similar number of individuals were recorded in the common reed stands (on average, 12.3 individuals per visit and per station), in the cattail stands (11.3) and in the short-height vegetation stands (13.0). More species were seen or heard in the common reed (43) and short-height vegetation (41) stands than in the cattail (32) stands.

Among generalist passerines, American yellow warbler was the most frequently recorded species (107 observations), followed by song sparrow (52). The average water depth was the only explanatory variable with a significant effect on site occupancy by generalists (Supporting Information Appendix S1). In both years, the site occupancy probability decreased with water depth (Table 1). For specialist passerines, marsh wren (256 observations) and marsh sparrow (211) were the most frequently recorded species. The percentage of the area of a station occupied by open water and, to a lesser extent, the average water depth were the variables with a significant effect on site occupancy, but this influence varied among species (Supporting Information Appendix S1). In general, the site occupancy probability for specialist passerines decreased with a rising area occupied by open water (2009 and 2010); this was especially remarkable for common yellowthroat in 2009 (Table 1). However, the presence of marsh wren increased in stations with more open water areas. For rails, presence of water was the only variable with a significant effect on site occupancy (2010 only) as more rails were observed when the water level was above the soil surface (Table 1).

The sampling period was the most influential variable on songbird abundance (according to AICc weights; Supporting Information Appendix S2); in general, the abundance of birds decreased through the sampling season in both years (Fig. 3). Birds were also more abundant in stations with deep water or with presence of water above the soil surface (Table 2). However, vegetation type did not have any significant influence on songbird abundance. Among generalist passerines, the vegetation type and the sampling period were the most influential variables on American yellow warbler and common grackle (Supporting Information

Table 1 Results of the site occupancy models of songbirds detected in point count stations located in freshwater marshes of southern Quebec

Species group	Explanatory variable[a]	β (SE) 2009	2010
Generalist passerines	Water depth	−2.523 (1.183)	−1.266 (0.345)
Marsh-specialist passerines	Open water areas (percentage of a station)	−1.868 (0.773)	−1.822 (0.908)
	Open water areas (percentage of a station)[a] marsh wren	2.949 (1.116)	–
	Open water areas (percentage of a station)[a] common yellowthroat	−1.581 (0.758)	–
Rails	Presence of water above the soil surface	–	2.326 (0.643)

The stations were sampled in spring/summer 2009 and 2010. The parameter estimate associated with each explanatory variable ($\beta \pm$ SE) was averaged across models and is only indicated when the 95% confidence interval of the slope (β) excluded 0.

[a]Indicates a model with an interaction between the variables.

SE, standard error.

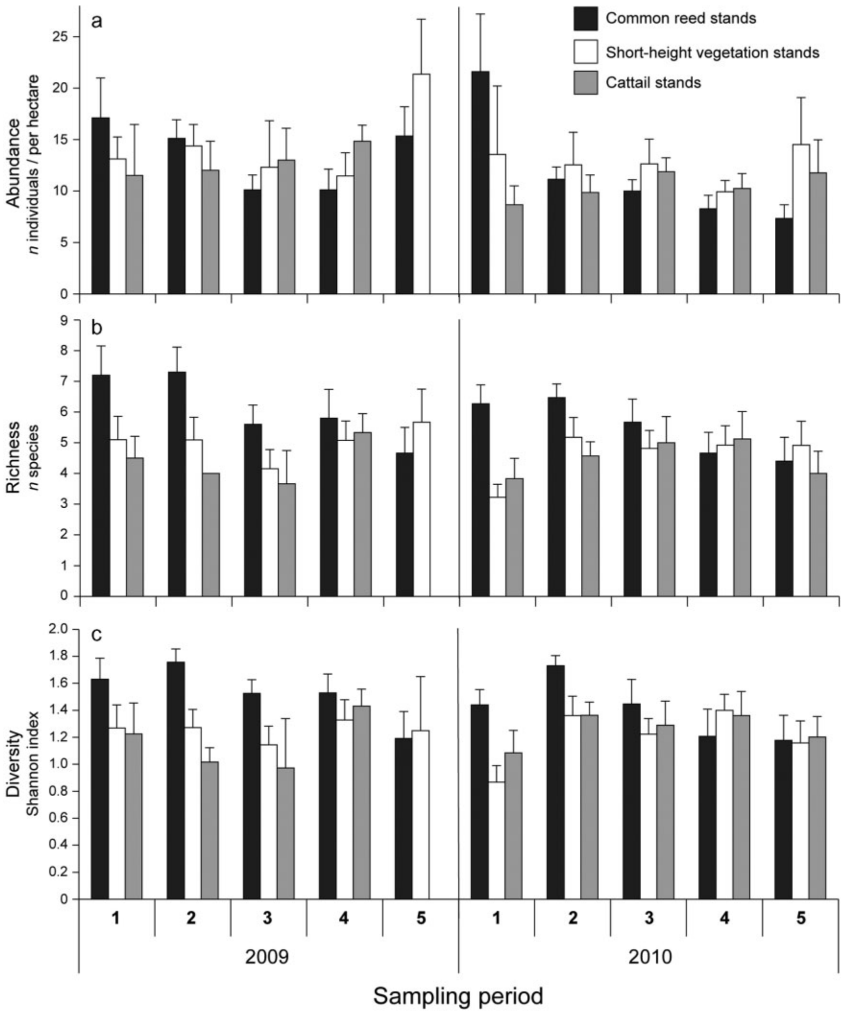

Figure 3 Mean (a) abundance, (b) richness and (c) diversity of songbirds sampled in point count stations located in southern Quebec freshwater marshes according to the vegetation type (dominated by common reed *Phragmites australis*, cattails *Typha* spp. or short-height vegetation). The sampling season in 2009 (May 22 to July 24) and 2010 (May 5 to July 26) was subdivided into five periods of about 15 days. Error bars indicate 1 standard error (SE). Note that no point count station with cattails was visited during the fifth sampling period in 2009.

Appendix S3). More warblers were observed in common reed stands than in the other vegetation types, and in stations with shallow water (Table 2). Common grackle was less numerous in short-height vegetation stands. Among specialist passerines, marsh sparrow was one of the rare species with a rising abundance during the spring/summer in 2009. The percentage of open water areas (both years) and the water depth (2009) had a negative influence on the abundance of this species (Table 2). The water depth also negatively influenced the abundance of the common yellowthroat (2010). Finally, the abundance of marsh wren was higher in cattail than in common reed stands (both years), and in stations with deep water and open water areas (2010).

Table 2 Results of the analysis of abundance, richness and diversity of songbirds detected in point count stations located in freshwater marshes of southern Quebec

Tested variable and species	Explanatory variable	β (SE) 2009	2010
Abundance: all species	Sampling period	–0.053 (0.027)	–0.092 (0.028)
	Presence of water above the soil surface	0.347 (0.161)	0.365 (0.112)
	Water depth	0.139 (0.064)	0.176 (0.056)
Abundance: American yellow warbler	Sampling period	[a]	–0.202 (0.096)
	Short-height vegetation type	[a]	–2.535 (0.763)
	Cattail vegetation type	[a]	–1.269 (0.600)
	Water depth	[a]	–0.926 (0.246)
Abundance: common grackle	Sampling period	–0.710 (0.107)	–0.249 (0.105)
Abundance: common yellowthroat	Water depth	[a]	–1.033 (0.187)
Abundance: marsh wren	Sampling period	–	0.156 (0.061)
	Cattail vegetation type	2.342 (0.709)	1.379 (0.469)
	Presence of water above the soil surface	–	1.431 (0.466)
	Water depth	–	0.786 (0.224)
Abundance: swamp sparrow	Sampling period	0.346 (0.099)	–
	Open water areas (percentage of a station)	–0.495 (0.175)	–0.820 (0.188)
	Water depth	–0.324 (0.126)	–
Abundance: Virginia rail	Presence of water above the soil surface	–	3.073 (1.119)
	Water depth	–	1.196 (0.374)
	Open water areas (percentage of a station)	–0.798 (0.327)	–
Richness: all species	Sampling period	–0.076 (0.027)	–
Diversity (Shannon index): all species	Sampling period	–0.065 (0.029)	–
	Short-height vegetation type	–	–0.226 (0.112)

The stations were sampled in spring/summer 2009 and 2010. The parameter estimate associated with each explanatory variable ($\beta \pm$ SE) was averaged across models and is only indicated when the 95% confidence interval of the slope (β) excluded 0.
[a]No analysis conducted because there were less than 50 observations.
SE, standard error.

In both years, the water-related variables were the most influential variables on the abundance of Virginia rail, the only rail species with a sufficient number of observations for analysis (Supporting Information Appendix S3). In 2009, Virginia rail abundance was lower in stations with more open water areas, whereas in 2010, a dry year, the abundance of this species was higher in stations with deep water and presence of water above the soil surface (Table 2).

The sampling period was the most influential variable for the richness and diversity of songbirds (Supporting Information Appendix S2). In 2009, the richness and diversity decreased during the spring/summer (Fig. 2; Table 2), but no other variable had a significant influence, with the exception of vegetation type in 2010, as the diversity of songbirds was lower in short-height vegetation stands than in the other vegetation types that year.

Waterbirds

Twenty-six visual count surveys were conducted in 2009 and 29 in 2010. The waterbirds recorded included 33 species, mostly ducks and geese (77% of records). The most abundant species were mallard *Anas platyrhynchos* and Canada goose *Branta canadensis* (especially at the first survey in 2010) for waterfowl and great blue heron *Ardea herodias* and great egret *Ardea alba* for waders. There was no significant difference in waterbird abundance and richness between invaded and non-invaded (reference group) marshes (Fig. 4; Supporting Information Appendix S4). In 2009, invaded marshes had a higher waterbird diversity than non-invaded marshes (ß = 0.116; SE = 0.054).

Discussion

Overall, we found few differences between common reed stands and other freshwater marsh vegetation assemblages for songbird abundance, richness and diversity. Similar results have been reported in the few studies conducted in freshwater marshes in New York and Ontario (McGlynn, 2006; Meyer *et al*., 2010). In our study, presence of water above the soil surface and water depth generally had more effects on bird assemblages than vegetation *per se*.

Generalist songbirds were not affected by common reed as expected (Wells *et al*., 2008; Meyer *et al*., 2010), and one species, American yellow warbler, was even more abundant in common reed than in the other vegetation types. This species nests in shrubs located near open areas, brooks and ponds and usually select large shrub stands to

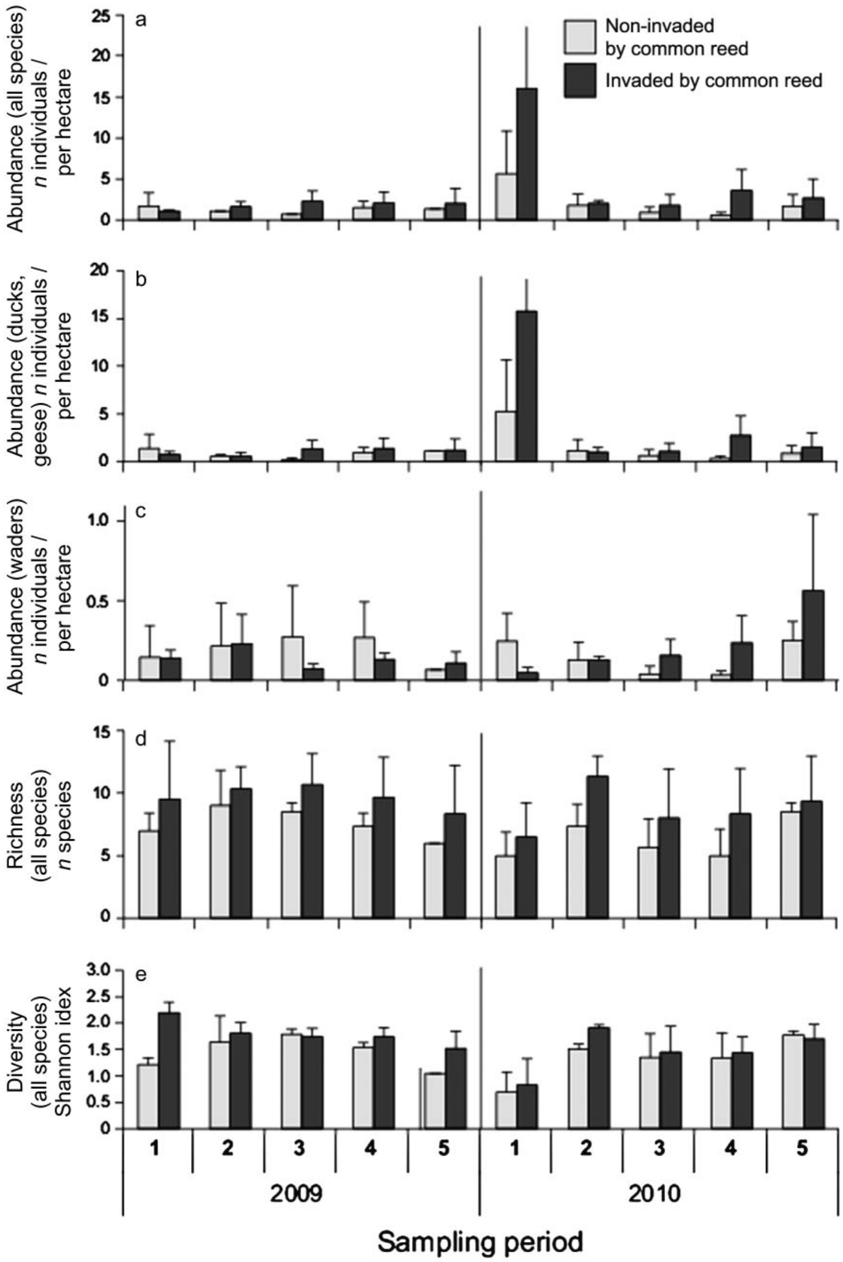

Figure 4 Mean (a) abundance (all species), (b) abundance of ducks and geese, (c) abundance of waders, and (d) richness and (e) diversity of waterbirds observed in freshwater marshes of southern Quebec that are invaded or non-invaded by common reed *Phragmites australis*. The sampling season in 2009 (May 22 to July 24) and 2010 (May 5 to July 26) was subdivided into five periods of about 15 days. Error bars indicate 1 standard error (SE).

enhance protection against predators (Knopf & Sedgwick, 1992). In the study area, almost all old fields and shrublands surrounding the marshes were converted into corn and soybean fields, especially during the last 30 years (Domon & Bouchard, 2007). Common reed stands form one of the few large vegetation assemblages remaining near water bodies; the warbler likely uses these stands as alternative nesting sites as their dense, tall and robust vegetation structure probably provides a suitable support for nests and a good protection against predators (Meyer *et al*., 2010).

Marsh wren was the only marsh-specialist bird species that was less abundant in common reed stands, especially compared with cattail stands. Most studies on the effect of common reed on marsh wren found negative impacts on its abundance or nesting activity (McGlynn, 2006; Wells *et al*., 2008; Meyer *et al*., 2010; Lazaran, Bocetti & Whyte, 2013), probably because common reed stands have low plant diversity and few appropriate nest materials (Verner & Engelsen, 1970; Meyer *et al*., 2010; Tozer, Nol & Abraham, 2010). Marsh wren was also the only passerine that preferred the wettest parts of the marshes. This preference could be associated either with a better protection from predators (Leonard & Picman, 1987; Picman, 1988; Jobin & Picman, 1997) or a higher abundance of prey (Tarr, Baber & Babbitt, 2005; Tozer *et al*., 2010).

The vegetation type had no significant effect on Virginia rail, a species that is not known to be associated with a specific plant assemblage during the reproduction period (Johnson & Dinsmore, 1986; Lor & Malecki, 2006). The abundance of this rail species was reduced in common reed stands in Connecticut tidal wetlands (Benoit & Askins, 1999), but stands in those brackishwater marshes had apparently a higher stem density than freshwater ones (Meyerson *et al*., 2000), which could represent a physical obstacle for birds moving on the ground or water surface like rails. In the freshwater marshes that we studied, the vegetation near the soil/water surface is not very dense in common reed stands, and thus, rails should be able to move through the common reed, unlike what we initially suspected. A finer analysis of the vegetation structure may thus be required to fully understand the role of common reed as a physical barrier for birds. On the other hand, water-related variables were influential on Virginia rail, but their effect was variable between years: in 2009, a year with water levels higher than normal in marshes (Larochelle, 2011), Virginia rail occupied the drier sections of the marshes, while in 2010, a year with very low water levels, it was confined to the wettest areas. Therefore, this species does not apparently use sites that are either too wet or too dry during the reproduction period (Lor & Malecki, 2006). In Wales, the abundance of the water rail *Rallus aquaticus*, a species that uses common reed beds for breeding, is mostly associated with the wettest parts of the beds, which probably reflects lower predation risk and higher food availability (Jenkins & Ormerod, 2002).

Data from visual counts do not support the hypothesis of a negative impact of common reed on waterfowl and waders, at least in marshes with less than 50% of their area invaded by the plant. This conclusion should nevertheless be considered with caution since birds were essentially observed from parts of the marshes without common reed. In fact, very few ducks and waders were observed inside common reed stands, probably because (1) they are hardly penetrable (Benoit & Askins, 1999); (2) they do not provide high-quality nesting material (Meyer *et al*., 2010); (3) they block the view and therefore hamper the detection of prey or predators (Gilbert *et al*., 2005; Kessler *et al*., 2011). Small-sized wading birds apparently use common reed stands for reproduction, but there is no evidence that large-sized waders (e.g. great blue heron or great egret) feed or nest in these stands (Parsons, 2003; Trocki & Paton, 2006). In summary, common reed stands do not prevent the use of non-invaded parts of the marshes by birds but may have a local effect for some waterbirds by reducing the availability of feeding and nesting sites.

This study adds to a growing body of evidence (see Schlossberg & King, 2010; Lavoie, 2010; Tavernia & Reed, 2012; Ma *et al*., 2013) showing that the relationship between invasive plants and birds is not straightforward. Common reed stands are clearly not barren zones devoid of birds as they are used by generalist and specialist marsh passerines for feeding and reproduction. In Europe, the probable origin of the invader (Plut *et al*., 2011; Meyerson & Cronin, 2013), common reed beds are used as nesting sites by a large number of bird species, including grebes, passerines, rails and small-sized waders (Bibby & Lunn, 1982; Tscharntke, 1992; Jenkins & Ormerod, 2002; Poulin, Lefebvre & Mauchamp, 2002; Gilbert *et al*., 2005). Common reed stands could thus potentially represent suitable habitats for related species in North America, as far as the invader does not locally reduce food resource for bird species (Poulin *et al*., 2002). Preliminary samplings of invertebrates conducted in the Beauharnois Canal marshes in 2010 (Gagnon Lupien, 2013) suggest that the total biomass of the invertebrates of the common reed beds was similar to that of the other vegetation types, although there were some differences in species composition; similar results have been reported for other freshwater wetlands invaded by the common reed (McGlynn, 2006; Kulesza *et al*., 2008; Holomuzki & Klarer, 2010). Other food sources for birds, especially for waders, are apparently not affected by the common reed in southern Quebec. There is no evidence of a negative effect of common reed presence on anuran populations at any life stage (Mazerolle, Perez & Brisson, 2014). The invasion of wetlands by the common reed does not seem to have a major effect on the relative abundance, growth and feeding of young northern pikes *Esox lucius*, one of the most important fish species of freshwater marshes (Larochelle, 2011). Consequently, the common reed is more likely to affect bird assemblages because of its effect on the vegetation structure of marshes than because of its effect on food resources.

Overall, the scant amount of data currently available makes it impossible to determine whether common reed stands constitute a favorable habitat for bird species in general, or for some specialists in particular, over the long term. It is also possible that, along the St. Lawrence River, the number and extent of common reed populations in freshwater marshes have not yet reached a threshold beyond which adverse effects of the invader on birds may be more significant. Moreover, little is known on the magnitude or the effects of common reed biomass accumulation in North American freshwater wetlands, which could strongly disturb the hydrology by elevating the marsh floor (Rooth, Stevenson & Cornwell, 2003). Several bird species, and especially rails, could be affected by such disturbance. Consequently, conservationists should be cautious and should not interpret our data as definitive evidence of a weak effect of the invasive common reed on freshwater marsh birds.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Site occupancy model selection for songbirds detected in point count stations located in freshwater marshes of southern Quebec. The stations were sampled in spring/summer 2009 and 2010. The c-hat value was established at 1. Only the best models (i.e. those with a ΔAICc value < 4 compared with the best model) are shown with their respective weight (ωAICc).

Appendix S2. Selection of mixed linear regression models for the abundance, richness and diversity of songbirds detected in point count stations located in freshwater marshes of southern Quebec. The stations were sampled in spring/summer 2009 and 2010. Only the best models (i.e. those with a ΔAICc value < 4 compared with the best model) are shown with their respective weight (ωAICc). Null models are also indicated.

Appendix S3. Selection of mixed linear regression models for the abundance of songbird species detected in point count stations located in freshwater marshes of southern Quebec. The stations were sampled in spring/summer 2009 and 2010. Only the best models (i.e. those with a ΔAICc value < 4 compared with the best model) are shown with their respective weight (ωAICc). Null models are also indicated.

Appendix S4. Selection of mixed linear regression models for the abundance, richness and diversity of waterfowl (ducks, geese) and waders detected in freshwater marshes of southern Quebec invaded (or not) by common reed *Phragmites australis*. The stations were sampled in spring/summer 2009 and 2010. Only the best models (i.e. those with a ΔAICc value < 4 compared with the best model) with their respective weight (ωAICc) are shown. Null models are also indicated.