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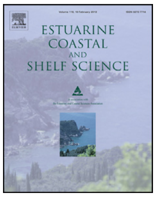

Avian response to tidal freshwater habitat creation by controlled reduced tide system

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ABSTRACT

Human activities have caused extensive loss of estuarine wetlands, and the restoration of functional habitats remains a challenging task given several physical constraints in strongly embanked estuaries. In the Schelde estuary (Belgium), a new tidal marsh restoration technique, Controlled Reduced Tide system (CRT), is being implemented in the freshwater zone. A polder area of 8.2 ha was equipped with a CRT to test the system functionality. Among different ecological compartments that are studied for assessing the CRT restoration success, avifauna was monitored over three years. The tidal regime generated a habitat gradient typical of tidal freshwater wetlands along which the distributions of bird and ecological groups were studied. 103 bird species were recorded over the three years. In addition to many generalist bird species, several specialist species typical of the North Sea coast were present. Thirty-nine species of local and/or international conservation interest were encountered, emphasising the importance of this habitat for certain species. Species communities and ecological groups were strongly habitat specific and non-randomly organized across habitats. Spatiotemporal analyses highlighted a rapid habitat colonization, and a subsequent stable habitat community structure across seasons in spite of strong seasonal species turnovers. Hence, these findings advocate CRT implementation as a means to effectively compensate for wetland habitat loss.

1. Introduction

Several decades of intense human activities in estuaries have increased the need to remedy their adverse effects. Present regulations and international directives compel decision-makers to safeguard and restore the ecological integrity of estuaries given the increasingly recognized value of ecosystem services these ecosystems provide (Elliott et al., 1999; Van den Bergh et al., 2005; Barbier et al., 2010). As a consequence, estuarine restoration plans increasingly are implemented, mainly in North America and Western Europe. In managing and evaluating these ecological restoration projects, monitoring different ecosystem compartments is a necessary post-implementation task to evaluate the restoration success. Birds are generally recognized as highly relevant indicators of habitat restoration and ecosystem and ecosystem functionality (Koskimies, 1989; Bernstein et al., 1991; Johnson, 2007; Latta and Faaborg, 2008). Many wetland bird species are known to be habitat specific and sensitive to hydrological variations (Roshier et al., 2002; Gonzáles-Gajardo et al., 2009). Functionally, as ecosystem regulators from upper trophic levels, bird abundance and community structure indicate ecosystem processes and habitat quality (Moreira, 1997; Atkinson, 2003; Johnson, 2007; Mendonça et al., 2007; Xiong et al., 2010).

In Europe, the North Sea coast is an important region along the East Atlantic flyway of migrant bird species, where the Schelde estuary (The Netherlands and Belgium) is one of the important stopovers. The international importance of the Schelde estuary is shown as 21 waterbird species, depending mainly on the presence of tidal flats and marshes, exceed regularly the 1% criterion of the Ramsar convention (Ysebaert et al., 2000). However, the Schelde estuary has been heavily impacted by expanding port facilities and embankments, and 16% of the habitat surface was lost during the twentieth century, particularly low marshes and tidal flats which lost more than 50% of their initial surface area (Meire et al., 2005). Although the Schelde estuary is protected under the European

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Birds and Habitats directives (2009/147/EC and 92/43/EEC, being part of the Natura 2000 network) and several national laws, harbour expansion still occurs and requires habitat compensation (Van den Bergh et al., 2005). Tidal flat and marsh restoration is essential to ensure conservation of the internationally important bird populations present.

In many cases, estuarine habitat restoration occurs by managed realignment which consists of a setback of the dike to increase estuarine surface area from previous land-claim (French, 2006). However, often these areas generally lie far below the mean high water level due to subsidence after embankment combined with sea level rise. This prevents the restoration of a complete flooding frequency gradient which ensures a diversity of successive estuarine habitats. Different techniques have been used, but none of them has been able to overcome this constraint (Beauchard et al., 2011). For instance, Atkinson et al. (2004) mentioned that despite the successful tidal flat bird community development following dike breaching in the UK, the area lacked the full range of biodiversity found in the surrounding natural intertidal habitats.

Since 2006, a new technique, the Controlled Reduced Tide system (CRT), has been implemented in a pilot project in the freshwater zone of the Schelde estuary to combine habitat restoration and storm flood protection (Maris et al., 2007). This generates a complete intertidal gradient (Beauchard et al., 2011), along which vegetation developed as typically encountered in natural tidal freshwater marshes (Jacobs et al., 2009). Hence, CRT is hypothesized to successfully promote bird community development among the newly created habitats.

It is however difficult to measure accurately the success of wildlife community restoration in the absence of reference sites, at least in large areas (McCoy and Mushinsky, 2002). In the freshwater part of the Schelde estuary, most low marshes have been lost due to embankments and shore reinforcements, and a complete habitat gradient no longer exist (Struyf et al., 2009). The current intertidal shores lack the gradual transition of bare mudflat to vegetated low, middle and high marshes and therefore these deteriorated habitats are unsuitable as a reference for evaluating the CRT system for estuarine habitat restoration (Meire et al., 2005). Only few bird studies on natural tidal freshwater zones along the North Sea coast allow a general comparison whereby the species encountered in these studies can be used as a reference pool. Instead, in the absence of reference marshes as a baseline, studying habitat occupancy of species based on their ecological preferences and attributes is likely the best approach for assessing restoration success (Moore et al., 1999; Brewer and Menzel, 2009). At the community level, multivariate procedures provide robust tools to detect non-random habitat occupancy (Wiens and Rotenberry, 1981; Gotelli and Graves, 1996). In this way, CRT habitat suitability can be consistently assessed since habitat requirements of bird species from the western Palearctic have been largely documented (Cramp, 1982).

Hence, avian response to CRT habitat creation can be evaluated by (a) comparing the patterns of ecological attributes of the observed and documented regional reference species pools, and (b) testing non-random habitat occupancy of species communities. Therefore, by investigating spatiotemporal bird species distributions, this study explores the dynamics of bird communities in the first CRT in order to appraise their response to the newly-created habitats and the relevance of further wide applications of the CRT technique in tidal wetland restoration.

2. Methods

2.1. Study area

The experimental area, the Lippenbroek polder, is located in the freshwater zone of the Schelde estuary (51°05′10″N; 4°10′20″E; Fig. 1). The CRT system has created the polder's tidal influence since March 1st, 2006. It covers an area of 8.2 ha, and is connected to the estuary by high inlet and low outlet culverts which produce a controlled tidal regime (see Cox et al. (2006), Maris et al. (2007) and Beauchard et al. (2011) for technical details); this design is expected to successfully produce ecological functioning and storm flood protection. The polder is completely flooded every spring tide, with a mean water height of 40 cm, whereas either no water or a limited amount enters at neap tide.

The polder used to be arable land like the adjacent ones where crops and poplars are still grown. Typical bird species occurring there are represented by non-wetland species such as *Buteo buteo*, *Columba palumbus*, *Corvus corone*, *Garrulus glandarius*, *Pica pica* and *Phasianus colchicus*; occasionally, duck species such as *Anas platyrhynchos* and *Tadorna tadorna* are encountered in the fields and marginal ditches (unpubl. obs.).

2.2. Habitats

During the first year (2006), vegetation surveys showed rapid changes in composition, density and vegetation height after the implementation of the tidal regime (Jacobs et al., 2009). In the three following years, further changes consisted only of plant species composition, with two exceptions. Firstly, dense monospecific Reed (*Phragmites australis*) and Cattail (*Typha latifolia*) patches extended. These zones were sufficiently homogeneous and categorized “Reed” (abbreviated R in results) and “Cattail” (C). Secondly, from spring 2008, a patch of single shoots of willow (*Salix* sp.) formed a 4 m high shrub whose canopy dominated the remnant forbs vegetation; this habitat was categorized “Shrub” (S; Fig. 1).

The largest part of the study area remained occupied by forbs. Its species composition was mostly dominated by Great Willowherb (*Epilobium hirsutum*), Purple Loosestrife (*Lythrum salicaria*), Pale Persicaria (*Polygonum lapathifolium*) or combinations of those. Their height varies between 0.5 and 2 m, and generally these zones were very dense; this habitat was categorized “Forbs” (F). In the central part of the study area, a dense forest-type patch, already present for several decades and persisting, was categorized “Willow” (W). It consisted mainly of *Salix* sp., but some poplars (*Populus* sp.) also persisted. This habitat is about 7 m high, very hard to penetrate and strongly shaded with almost no understory of annuals. Scattered throughout the area, some isolated trees (*Salix* sp. and *Populus* sp.) were categorized “Isolated tree” (I). All the vegetated habitats remained constantly available for bird foliage specialists since the highest mean water levels did not exceed 40 cm. Finally, in about 40% of the area, only isolated plants were found, but the general aspect is that of a bare ground. Recent studies showed the high silty nature of deposited particles (Beauchard et al., 2013), and this habitat was therefore categorized “Mudflat” (M). Although in recent years its total surface has declined due to *Phragmites australis* extension, the main zonation has remained generally unchanged during the study period.

Summarizing the vegetation development, Mudflat (M), Cattail (C) and Reed (R) were the most characteristic wetland habitats which emerged after CRT implementation. Forbs (F) were either remnant or modified in term of species composition, and Shrub (S) developed from Forbs. Willow (W) and Isolated trees (I) were already present before CRT implementation. These seven co-occurring habitats, ranging from aquatic to terrestrial conditions, formed a habitat gradient, typical of natural tidal freshwater wetlands (Struyf et al., 2009). Hence, they provide an experimental context of space-for-time substitution (Pickett, 1989) whereby the avifaunal response to CRT implementation was studied.

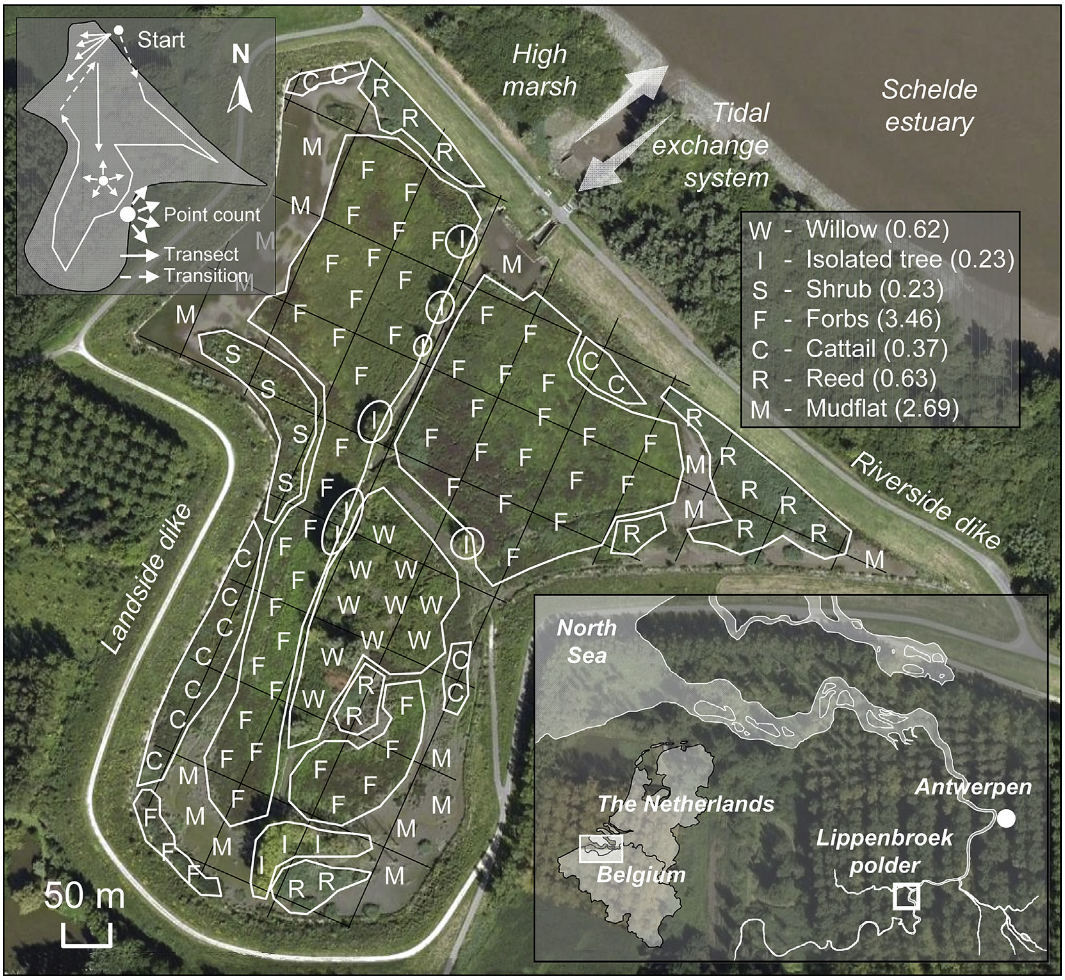

Fig. 1. Aerial view of the experimental polder. Bottom-right insert: location map of the polder along the Schelde estuary. Top-left insert: census path. Top-right insert: habitat abbreviations; numbers in brackets indicate the surface area in ha. Black grid: quadrats used for locating observations (for clarity, numbers are not mentioned). Photograph: Google Earth, 2009.

2.3. *Monitoring*

Bird surveys were conducted weekly from autumn 2006 to winter 2010 with two types of observations: a regular monitoring from December 21st, 2006 to March 18th, 2010, representing the core of this study, complemented with anecdotal observations during other field visits since mid-autumn 2006. In order to account for the variability in tidal conditions, bird censuses were conducted in four different tidal states: spring high tide, neap low tide, spring low tide and neap high tide. Since bird detection probability has been shown to be higher in the morning in many ecosystems (Robbins, 1981; Skirvin, 1981; Smith and Twedt, 1999; Nadeau et al., 2008), censuses were done mostly between 6:30 and 14:00, depending on the tide; over the whole study period, this resulted in 166 regular censuses ensured by the same observer (O. Beauchard), except 6 times (observer S. Jacobs).

Censuses consisted of a combination of point counts (northernmost dike and central wood of the polder, Fig. 1) and transect counts covering the main area and crossing the main habitat patches in order to flush birds undetectable by passive observation. In dense vegetation, an active procedure generating noise disturbance (completed by hand-clapping) was used since several marsh bird species stay concealed within dense vegetation (Gregory et al., 2004). Quantitative records comprised visual (identifications helped by 10 × 50 binoculars) and auditory observations of resting, singing, foraging and escaping individuals; records were spatially referenced by using a map (numbered quadrats, Fig. 1). In spring and summer, “pishing” sounds (Zimmerling, 2005) were used in dense vegetation patches to effectively detect breeding species such as *Acrocephalus scirpaceus* and *Acrocephalus palustris* by eliciting defensive behaviour from adults. Census duration ranged between 45 and 120 min depending on species richness and abundances.

Each census started from the dike at the north count point (Fig. 1, “Start”). This point faces a large open mudflat where frequent flocks of waterbirds were counted with more precision from the dike than arriving from the south side of the mudflat after the successive disturbing counts through the marsh. Then, census was followed by transect counts, consisting in slow walks and brief pauses to look and listen along transects (Emlen, 1971); long stops were avoided to reduce the risk of double-counting. The north mudflat was considered a second time only if new species were encountered. Census was achieved by a last point count after penetrating the central wood (circa 5–10 min). Some flushed birds either left the marsh or stayed in the marsh where landing locations were noted (quadrats, Fig. 1) in order to avoid that individuals were counted twice. Distance counting was unlimited, and records could comprise observations behind (in case of new species) and ahead of the advancing observer. Given the small surface area of habitat patches and the complete census coverage of the marsh, abundances were analysed without correction since distance sampling techniques are generally inefficient in small areas (Buckland et al., 2008).

2.4. Data analyses

Species richness and ecological group distributions were studied per habitat. Daily species abundances were averaged per season (13 calendar-based seasons over the 3 years for each habitat). Cumulative species richness curves were plotted for the whole study period in order to assess temporal community responses to the newly-created habitats. Species ecological characteristics were considered based on their affinity for wetlands (W, wetland specialist; nW, wetland non-specialist) and on their foraging status (A, air; F, foliage; FG, foliage and ground; G, ground); information was derived from Cramp (1982); see Table 1. Along the habitat gradient, analyses of variance (ANOVA) were used to test habitat effect on proportion of ecological groups. The CRT species pool was then compared to a reference species pool compiled from three reported regional inventories conducted in tidal freshwater wetlands along the North Sea coast, totalling more than 700 ha (Strucker, 1996; Temmerman, 1992; Van Waeyenberge et al., 1999). Species from this reference list were attributed ecological characteristics based on the same wetland and foraging classification. The ecological similarity between group proportions of the two species pools were tested by Chi-square and Fisher's exact tests. For this analysis, only species typically encountered in tidal freshwater wetlands were considered as wetland specialists, and rare and occasional wetland and non-wetland specialists were discarded.

Prior to community structure description, a quantitative approach was used to disentangle the effects of year, season and tide on community structure (composition and abundance) in each habitat. The relative effects were quantified by between-group analyses (Dolédec and Chessel, 1987) applied to sample × species matrices (one matrix per habitat; *log*-transformed abundances). Species abundances in each sample were averaged for each combination of year × season × tide (last winter season excluded in order to balance the observation plan by ensuring 4 seasons × 3 years). Since Shrub habitat was not present before spring 2008, analyses of this habitat were done from spring 2008 to winter 2010. In each analysis, the matrix was column-centred so that the resulting principal component analysis (centred PCA) ordinates communities according to niche breadth (Dray et al., 2003). Between-group analysis returns the amount of explained inertia of the PCA (i.e. explained multidimensional variance) by the considered factor. Then, effect significance was tested by a randomization procedure based on 9999 random permutations on the matrix lines (Heo and Gabriel, 1997). The same procedure was then applied on the whole dataset (samples as combinations of habitat × year × season × tide) to identify the factors which dominantly structured the communities at the marsh scale.

The exploration of species community structure may be rendered difficult by interactive effects of the spatiotemporal factors. Therefore, possible confounding effects were circumvented by applying Foucart's Correspondence Analyses (FCA; Pavoine et al., 2007) to the dataset in order to explore species distributions among the CRT habitats, and how habitats ordinate as regard to the habitat gradient. Data were arranged in a global sample × species matrix in which species abundances were averaged per combination of habitat and season given the strong migratory nature of waterbirds in the Schelde estuary (Ysebaert et al., 2000). From the four season matrices (habitats × species), FCA computes an average matrix to construct a reference system of axes. Finally, samples and species ordinations results from the projections of the four matrices onto this reference; hence, the variability of habitat ordination can be explored from one season to another without undergoing seasonal effect. The interpretation of the results was completed by Jaccard's similarity index.

Computations and graphical representations were performed in R software (R Development Core Team, 2009) and multivariate analysis on *ade4* package available in R (Chessel et al., 2004; Dray et al., 2007).

3. Results

3.1. Avifaunal description and comparison between CRT and reference species pools

Over the whole study period, a total of 13 013 individual birds were counted during the regular censuses (mean daily count = 78.4 ± 50.1 S.D., corresponding to 9.6 ± 6.1 S.D. birds.ha^{-1} on average). With additional observations, this encompassed 103 species, among which 94 were encountered during the regular censuses (mean daily species richness = 13.7 ± 4.1 S.D., corresponding to 1.7 ± 0.5 S.D. species.ha^{-1}). The overall CRT fauna is presented in Table 1. Despite the disturbing nature of the counting (51% of escapements), 81 species were observed at least once in foraging activity (27% of the observations); resting and other activities (e.g. singing, territoriality and breeding) accounted for 11 and 11% of the observations respectively. Among the 21 bird species of international importance in the Schelde estuary (Ysebaert et al., 2000), 12 of them were observed foraging in the CRT, and 4 (*Anas crecca*, *Anas strepera*, *Anas platyrhynchos*, and *Tadorna tadorna*) were among the 10 dominant species encountered during the study period and accounted for 50% of the total abundance. Additionally, 14 species of concern listed by the European Bird Directive (1% of all observations) and 21 species from the Flemish red list (17% of all observations) were encountered.

Species richness patterns exhibited a stronger habitat effect than seasonality (Fig. 2A). Globally, Willow and Forbs were the richest habitats (circa 20 species), followed by Mudflat (circa 15 species) and Isolated tree (circa 10 species); the other habitats accommodated less than 10 species. On average, seasonal species richness pattern was similar between Isolated tree, Willow and Shrub where number of species increased from spring to autumn, and reaching its minimum in winter. Forbs and Mudflat exhibited a seasonality marked by a higher number of species in spring and summer. The pattern was similar between Reed and Cattail where spring and autumn maxima opposed to summer and winter minima. Over the whole study period, the richest habitats (W, F and M) and Shrub accumulated more than 75% of their species pool after one year, whereas Reed and Cattail required twice more time (Fig. 2B).

Abundance was significantly correlated to species richness ($n = 86$, $r = 0.84$, $p < 0.001$). The number of wetland specific individuals reached 84% of the total (Fig. 3). Non-wetland species proportions dominated in Isolated tree, Willow and Shrub whereas the dominance switched to wetland species in the other habitats. This pattern reflected a clear increase in the proportions of wetland specialists from the most terrestrial vegetation to the newly created wetland habitats (ANOVA: $F = 28.0$, $p < 0.0001$). Whereas Isolated tree, Willow and Shrub were more characterized by ubiquists (FG group; $F = 23.8$, $p < 0.0001$), birds with a ground affinity largely dominated from Forbs to Mudflat (G group; $F = 34.7$, $p < 0.0001$). Foliage specialists proportions (F group) also exhibited significant differences ($F = 14.6$, $p < 0.0001$), with minimum values in Forbs and Mudflat (almost absent), whereas they were similarly distributed in the rest of the habitats. Air foragers were excluded from the analysis as they were encountered in a small proportion (3 species, 16 observations). Globally, whereas non-wetland species were

Table 1
Species characteristics and occurrences. Numbers represent the total amount of observations over the study period. Foraging status: A, air specialist; F, foliage specialist; FG, foliage and ground ubiquist; G, ground specialist. Trophic status: H, herbivore; G, granivore; SO, small omnivore; SC, small carnivore; LO, large omnivore; LC, large carnivore. Migratory status: P, permanent resident; S, summer (and spring); W, winter (and autumn). Ramsar status: X indicates international importance based on the Ramsar convention criterion applied to the Schelde estuary. EU status: X indicates listing in annex I of the European Directive 2009/147/EC. Flemish status (Devos et al., 2004): D, declining; R, rare; V, vulnerable; T, threatened; TE, threatened to extinction. Common names: * indicates species which were encountered outside the regular censuses; they were not considered in the analyses.

Common name	Latin name	Wetland status	Foraging status	Trophic status	Residential status	Ramsar status	EU status	Flemish status	Isolated tree	Willow	Shrub	Forbs	Reed	Cattail	Mudflat
Sparrowhawk	*Accipiter nisus*		FG	LC	P				2	1					
Marsh Warbler	*Acrocephalus palustris*	X	F	SC	S				2	1	15	123	7	3	
Sedge Warbler	*Acrocephalus schoenobaenus*	X	F	SC	S			T					1		
Reed Warbler	*Acrocephalus scirpaceus*	X	F	SC	S					2	4	38	253	38	2
Common Sandpiper	*Actitis hypoleucos*	X	G	SC	S							3			12
Long-tailed Tit	*Aegithalos caudatus*		F	SC	P				55	182	44	49	28		
Common Kingfisher	*Alcedo atthis*	X	G	SC	P		X		16	37	3	8	1		4
Egyptian Goose	*Alopochen aegyptiacus*	X	G	H	P										30
Pintail	*Anas acuta*	X	G	H	W	X		R							1
Northern Shoveler*	*Anas clypeata*	X	G	H	W										2
Common Teal	*Anas crecca*	X	G	SO	W	X				543		1135	39	10	1769
Mallard	*Anas platyrhynchos*	X	G	SO	P	X				155	4	671	7	7	391
Gadwall	*Anas strepera*	X	G	H	S	X				43		495	2	5	473
Greylag Goose	*Anser anser*	X	G	H	W	X									3
Meadow Pipit*	*Anthus pratensis*	X	G	SC	P			T					1		
Water Pipit	*Anthus spinoletta*	X	G	SC	W							3			
Common Swift	*Apus apus*		A	SC	S							3			
Grey Heron	*Ardea cinerea*	X	G	LC	P				4	70		22	2		62
Long-eared Owl*	*Asio otus*		FG	LC	P					1					
Tufted Duck	*Aythya fuligula*	X	G	SO	W							2			
Canada Goose	*Branta canadensis*	X	G	H	P							7			74
Common Buzzard	*Buteo buteo*		FG	LC	P				2	6		9			
Linnet	*Carduelis cannabina*		F	G	P			D	2	8		40			
Goldfinch	*Carduelis carduelis*		F	G	P				14	3		2			
Greenfinch	*Carduelis chloris*		F	SO	P				11	12		1			
Short-toed Treecreeper	*Certhia brachydactyla*		F	SC	P					8					
Cetti's Warbler	*Cettia cetti*	X	F	SC	S			R			1	1	4		
Little Ringed Plover	*Charadrius dubius*	X	G	SC	S										1
Ringed Plover	*Charadrius hiaticula*	X	G	SC	S	X		R							5
Western Marsh Harrier	*Circus aeruginosus*	X	FG	LC	P		X					3			
Hen Harrier	*Circus cyaneus*		FG	LC	P		X					4			
Rock Dove	*Columba livia*		FG	G	P					2					
Stock Dove	*Columba oenas*		FG	SO	P										1
Wood Pigeon	*Columba palumbus*		FG	G	P				16	65		33		1	2
Carrion Crow	*Corvus corone*		FG	LO	P				13	11		9			1
Cuckoo	*Cuculus canorus*		F	SC	S			D	1						
Blue Tit	*Cyanistes caeruleus*		F	SO	P				11	40	11	15	30	4	
House Martin	*Delichon urbicum*		A	SC	S			V							3
Great spotted Woodpecker	*Dendrocopos major*		F	SC	P				7	16					
Lesser spotted Woodpecker	*Dendrocopos minor*		F	SC	P					1					
Great White Egret*	*Egretta alba*	X	G	LC	S		X								1
Little Egret	*Egretta garzetta*	X	G	LC	S		X	R							1
Reed Bunting	*Emberiza schoeniclus*	X	F	SO	W			T	3	20	7	522	172	6	
European Robin	*Erithacus rubecula*		FG	SO	P				11	37	8	73	4	1	
Eurasian Hobby	*Falco subbuteo*		F	LC	S										1
Rock Kestrel	*Falco tinnunculus*		FG	LC	P				12	7		9			
Chaffinch	*Fringilla coelebs*		FG	G	P				43	108		55	1		
Brambling	*Fringilla montifringilla*		FG	G	W					2		2			
Coot	*Fulica atra*	X	G	SO	P					4		13	1	6	13

Common Snipe	*Gallinago gallinago*	X	G	SC	W			TE			33	894	262	5	163
Common Moorhen	*Gallinula chloropus*	X	G	SO	P					102	5	263	38	26	264
Jay	*Garrulus glandarius*		FG	LO	P				12	28					
Eurasian Oystercatcher	*Haematopus ostralegus*	X	G	SC	S	X									15
Barn Swallow	*Hirundo rustica*		A	SC	S			D					5		5
Herring Gull	*Larus argentatus*	X	G	LO	P										5
Common black-headed Gull	*Larus ridibundus*	X	G	LO	P										199
Grasshopper Warbler	*Locustella naevia*	X	F	SC	S								3	1	
Blue Throat	*Luscinia svecica*	X	F	SC	S		X				1	25	6	1	
Jack Snipe	*Lymnocryptes minimus*	X	G	SO	W		X					2			
Smew	*Mergellus albellus*	X	G	LC	W		X								1
White Wagtail	*Motacilla alba*	X	G	SC	S										7
Red-crested Pochard	*Netta rufina*	X	G	SC	W							2			
Night Heron	*Nycticorax nycticorax*	X	G	LC	S		X	R		1					
Eurasian Golden Oriole	*Oriolus oriolus*		F	SO	S			T		1					
Osprey*	*Pandion haliaetus*	X	G	LC	P		X								1
Bearded Reedling	*Panurus biarmicus*	X	F	SO	P			R				27	14	8	
Great Tit	*Parus major*		F	SO	P				19	55	5	13	1		
Eurasian Tree Sparrow	*Passer montanus*		F	SO	P			D		5					
Great Cormorant	*Phalacrocorax carbo*	X	G	LC	P				2						10
Common Pheasant	*Phasianus colchicus*		G	LO	P					4		38	7		
Ruff*	*Philomachus pugnax*	X	G	SC	S		X								1
Northern Chiffchaff	*Phylloscopus collybita*		F	SC	S					28	10	19	3	2	
Black-billed Magpie	*Pica pica*		FG	LO	P				13	24	1	1			1
Green Woodpecker	*Picus viridis*		FG	SO	P				11	4	2				
Spoonbill	*Platalea leucorodia*	X	G	LC	S	X	X								2
Great Crested Grebe*	*Podiceps cristatus*	X	G	LC	P										1
Willow Tit	*Poecile montanus*		F	SO	P			V		4					
Marsh Tit	*Poecile palustris*		F	SC	P				1						
Dunnock	*Prunella modularis*		FG	SO	P				11	8	4	19	2		
Water Rail	*Rallus aquaticus*	X	G	SO	W					1	1	32	2		
Pied Avocet	*Recurvirostra avosetta*	X	G	SC	P	X	X	V							2
Goldcrest	*Regulus regulus*		F	SC	P					3		3		1	
European Stonechat	*Saxicola torquata*		F	SC	S								3		
Eurasian Woodcock	*Scolopax rusticola*	X	G	SO	P										
Common Tern	*Sterna hirundo*	X	G	LC	S		X	V				1			8
European Turtle-dove*	*Streptopelia turtur*		FG	G	S			T		1					
Common Starling	*Sturnus vulgaris*		FG	SO	P							1			
Blackcap	*Sylvia atricapilla*		F	SO	S				3			3			
Garden Warbler	*Sylvia borin*		F	SO	S				4	22	1	1			
Common Whitethroat	*Sylvia communist*		F	SO	S				9	7	1	41		1	
Little Grebe	*Tachybaptus ruficollis*	X	G	LC	P										2
Common Shelduck	*Tadorna tadorna*	X	G	SC	S	X				1		116			628
Spotted Redshank*	*Tringa erythropus*	X	G	SC	S	X									5
Wood Sandpiper	*Tringa glareola*	X	G	SC	S		X								6
Common Greenshank	*Tringa nebularia*	X	G	SC	S							3			19
Green Sandpiper	*Tringa ochropus*	X	G	SC	P							3			112
Common Redshank	*Tringa tetanus*	X	G	SC	S	X		V				1			5
Wren	*Troglodytes troglodytes*		F	SC	P				4	64	7	81	13	9	
Redwing	*Turdus iliacus*		FG	SO	W				10						
Blackbird	*Turdus merula*		FG	SO	P				19	25	7	143			
Song Thrush	*Turdus philomelos*		FG	SO	P				2	5	1	47			
Mistle Thrush	*Turdus viscivorus*		FG	SO	P					2		3			
Lapwing	*Vanellus vanellus*	X	G	SC	P							53			180

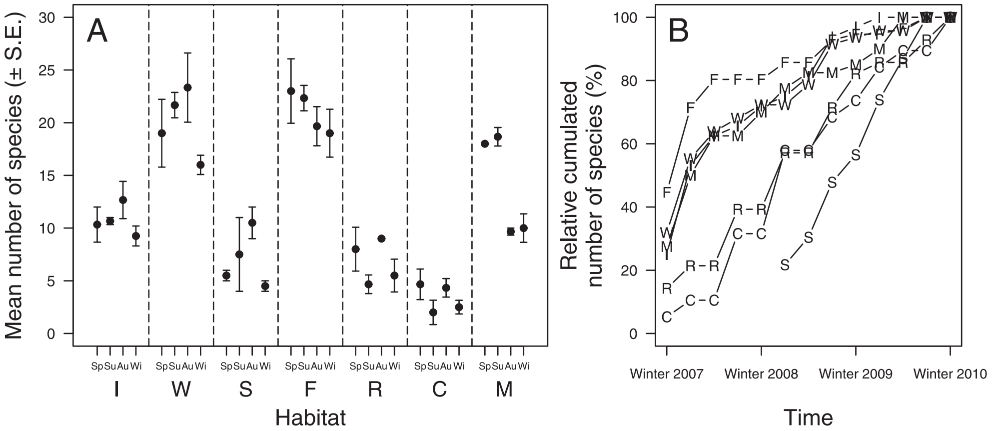

Fig. 2. Spatiotemporal pattern of species richness. A) Number of species per habitat from spring ("Sp") to winter ("Wi"); I, Isolated tree; W, Willow; S, Shrub; F, Forbs; R, Reed; C, Cattail; M, Mudflat. B) Relative species accumulation per habitat over the study period.

mainly permanent resident and dominated by foliage specialists and ubiquists, wetland species were mainly migratory and dominated by ground specialists (Table 2).

All CRT species were found among the 121 species from the reference pool (Table A.1), except *Poecile palustris*. CRT and reference species ecological groups exhibited similar proportions (Table 2). Proportions of CRT and reference wetland specialists were not significantly independent (Chi-square test, $p > 0.05$). Within wetland specialists, neither proportions of residential groups nor proportions of foraging groups significantly differed between the two species pools (Chi-square and Fisher's tests, $p > 0.05$).

3.2. Spatiotemporal determinants of community structure

No significant year effect was detected on community structure, except in Cattail and Reed, albeit rather weak (Table 3). In contrast, all habitats experienced a strongly significant seasonality. Tidal effect was more variable, but significant only on Forbs and Mudflat community structures. When considering the whole study area, habitat had by far the strongest effect, followed by season. In addition, year and tide engendered a non- or weakly significant effect.

3.3. CRT habitat community structure

FCA underlined the clear habitat effect (Fig. 4, left panel), and a remarkable spatial stability across seasons depicted by the relatively constant positions of habitats (Fig. 4, right panels). This stable configuration also exhibited a constant amplitude from one season to another. This reflected a stable faunistic dissimilarity between habitats despite a strong seasonal species turnover in each habitat ranging between 10 and 60% (Table A.2); only Reed and Cattail communities were similar. The first axis arranged three groups of habitats along the habitat gradient, (Fig. 4, from right to left): Mudflat, helophytes (Cattail, Reed and Forbs) and tree-like habitats (Shrub, Willow and Isolated tree). The Mudflat community was characterized by ground specialists such as gulls (e.g. *Chroicocephalus ridibundus*), waders (e.g. *Tringa* spp., *Haematopus ostralegus*)

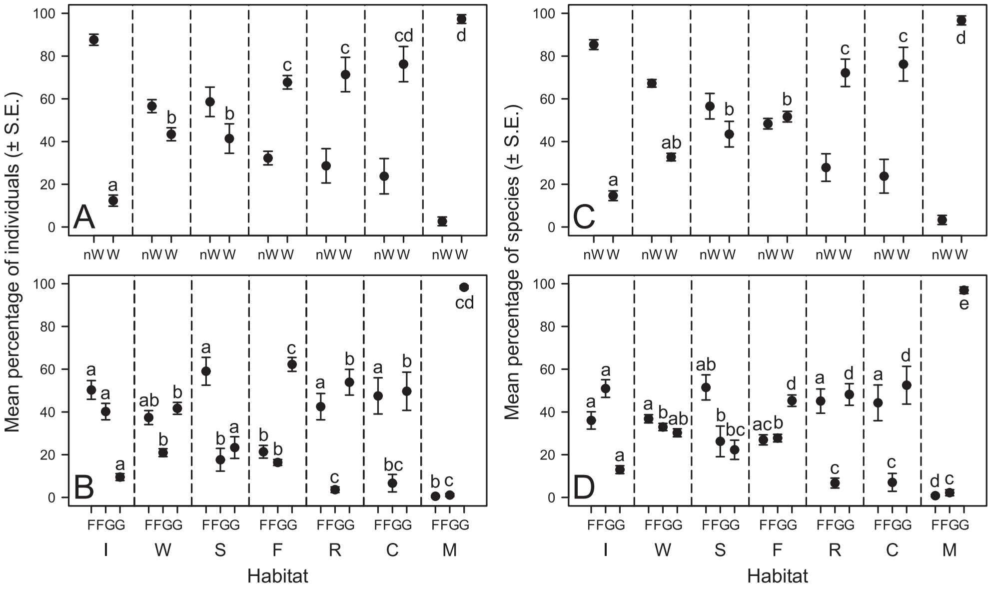

Fig. 3. Mean proportion of individuals and species per habitat and status. A and B) nW, non-wetland species; W, wetland species. C and D) F, foliage specialist; FG, foliage and ground ubiquist; G, ground specialist. See Fig. 2 for habitat codes. Significance of habitat effect on proportions within each group was tested; absence of common letter indicates a significant difference according to a Tukey HSD test at the rejection level $\alpha = 0.05$.

Table 2
Numbers and proportions of species per ecological group in CRT and reference species pools. Foraging status: A, air specialist; F, foliage specialist; FG, foliage and ground ubiquist; G, ground specialist. Percentages are expressed relatively to the total number of species in each pool.

		Non-wetland species								Wetland species							
		Permanent resident				Migratory resident				Permanent resident				Migratory resident			
		A	F	FG	G	A	F	FG	G	A	F	FG	G	A	F	FG	G
Number of species	Reference	0	13	17	3	2	10	8	0	0	2	1	21	0	9	1	34
	CRT	0	11	17	0	3	7	3	0	0	2	1	17	0	7	0	24
Proportion of species (%)	Reference	0.0	10.8	14.2	2.5	1.7	8.3	6.7	0.0	0.0	1.7	0.8	17.5	0.0	7.5	0.8	28.3
	CRT	0.0	12.0	18.5	0.0	3.3	7.6	3.3	0.0	0.0	2.2	1.1	18.5	0.0	7.6	0.0	26.1

and anatids (e.g. *Branta canadensis*, *Alopochen aegyptiacus*). Among the latter, *Anas crecca* ensured a transition toward the successive habitats by occupying also Forbs. In this habitat, *Gallinago gallinago* and *Panurus biarmicus* were characteristic, albeit frequently encountered in Reed and Cattail in which *Acrocephalus scirpaceus* was the most specific species. Communities in Isolated tree, Willow and Shrub were characterized by forest species (e.g. *Garrulus glandarius*, *Aegithalos caudatus*) among which *A. caudatus*, as a foliage specialist, ensured a faunistic transition to helophyte habitats.

The second axis exhibited a similar pattern, but contrasted by the position of Mudflat, closer to tree-like habitats. *Acrocephalus scirpaceus*, specific to Reed beds (narrow spatial niche), conferred a high foliage specificity to Reed and Cattails. Conversely, Mudflat, Willow and Isolated tree were visited by permanent resident species able to forage or roost in foliage and/or on the ground (i.e. large spatial niche): omnivores and carnivores such as *Ardea cinerea*, *Corvus corone*, *Phalacrocorax carbo* and *Pica pica*; *Columba palumbus* as ground and foliage opportunists; *Alcedo atthis* fishing in Willow as well as on Mudflat at high tide. Indeed, the strongest correlation to the second axis was obtained with the proportion of permanent species with an affinity for ground (Fig. 4, upper insert). Concurrently, both axes clearly discriminated ecological groups (Fig. 4, lower insert).

Table 3
Effects of spatiotemporal factors on community structure. Explained inertia denotes the amount of explained multidimentional variance of community structure by the considered factor in each between-group analysis.

Effect	Habitat	Explained inertia (%)	*p*
Year	Isolated tree	5.1	0.2055
	Wood	4.8	0.2762
	Shrub	4.4	0.1968
	Forbs	5.4	0.1629
	Reed	6.9	0.0430
	Cattail	6.6	0.0461
	Mudflat	4.3	0.4154
Season	Isolated tree	10.2	0.0101
	Wood	19.8	$<$ 0.0001
	Shrub	22.0	0.0019
	Forbs	27.0	$<$ 0.0001
	Reed	26.3	$<$ 0.0001
	Cattail	14.5	$<$ 0.0004
	Mudflat	21.0	$<$ 0.0001
Tide	Isolated tree	8.5	0.0682
	Wood	8.9	0.0539
	Shrub	6.5	0.8976
	Forbs	12.7	0.0012
	Reed	3.2	0.9968
	Cattail	5.7	0.6576
	Mudflat	9.9	0.0214
Whole data set			
Year		$<$1.0	0.2215
Season		5.5	$<$ 0.0001
Tide		1.5	0.0218
Habitat		29.1	$<$ 0.0001

4. Discussion

4.1. Potential monitoring drawbacks

In this study, given possible environmental and temporal influences on bird species community dynamics, the monitoring was designed to account for community change between habitats across years, seasons and tidal contexts. On the small surface of the study area, censuses were conducted weekly to avoid excessive disturbance, and in the morning given the higher bird detectability at that time of the day. Since bird detectability can vary among habitats and species, detection bias may have occurred, especially for cryptic species such as *Lymnocryptes minimus*, *Rallus aquaticus* and *Nycticorax nycticorax*. Indeed, Courtney and Gibbs (2005) demonstrated that using call-broadcast slightly increased detection rate of several species of rails and herons. Although *L. minimus*, *R. aquaticus* and *N. nycticorax* were detected in the CRT, their abundance might have been underestimated. This could have been the case also for *Porzana porzana* which has not been encountered over the three years, but was present in the reference species pool. Nevertheless, *L. minimus*, *N. nycticorax* and *P. porzana* are rare in Flanders (Devos et al., 2004). In addition, irrespective of analytical considerations, higher cryptic wetland specialist detectability and abundances would have probably strengthened the habitat effect, already significant following the counting method used here.

Observed species richness and abundances might have been constrained by the small surface area of the study site (8.2 ha). Surface area is known to be a limiting factor of species richness and abundance in marsh ecosystems (Brown and Dinsmore, 1986; Craig and Beal, 1992), where small surface areas may increase adverse edge effects on sensitive species through increased risk of predation, and especially disturbance due to human presence (Benoit and Askins, 2002). Influences on abundance and species richness appear likely since frequent walking and cycling passages occur along the dike surrounding the study area. Large marsh surface areas ensure buffer zones which minimize disturbance to sensitive birds such as waders for which flush distances can reach several tens metres (Burger, 1981; Rodgers and Smith, 1997).

Also, patterns of habitat species richness could have been biased due to unequal habitat surface area and perimeter; however, these parameters were not significantly correlated to the number of species ($p > 0.05$). The number of species observed in the CRT was less than the compiled reference list, but most of the species typical of the natural tidal freshwater marshes of the North Sea coast were encountered in the CRT. Several reasons may explain the lower CRT species richness such as habitat size requirement and isolation, especially concerning colonial species (Platteeuw et al., 2010). In addition, most of the reference species are derived from a study along a tidal river that includes habitats atypical of tidal marshes: river channel and residential zones (non-tidal), and managed habitats such as tidal coppices and meadows (Strucker, 1996). Despite this, no difference was found between the functional structures of

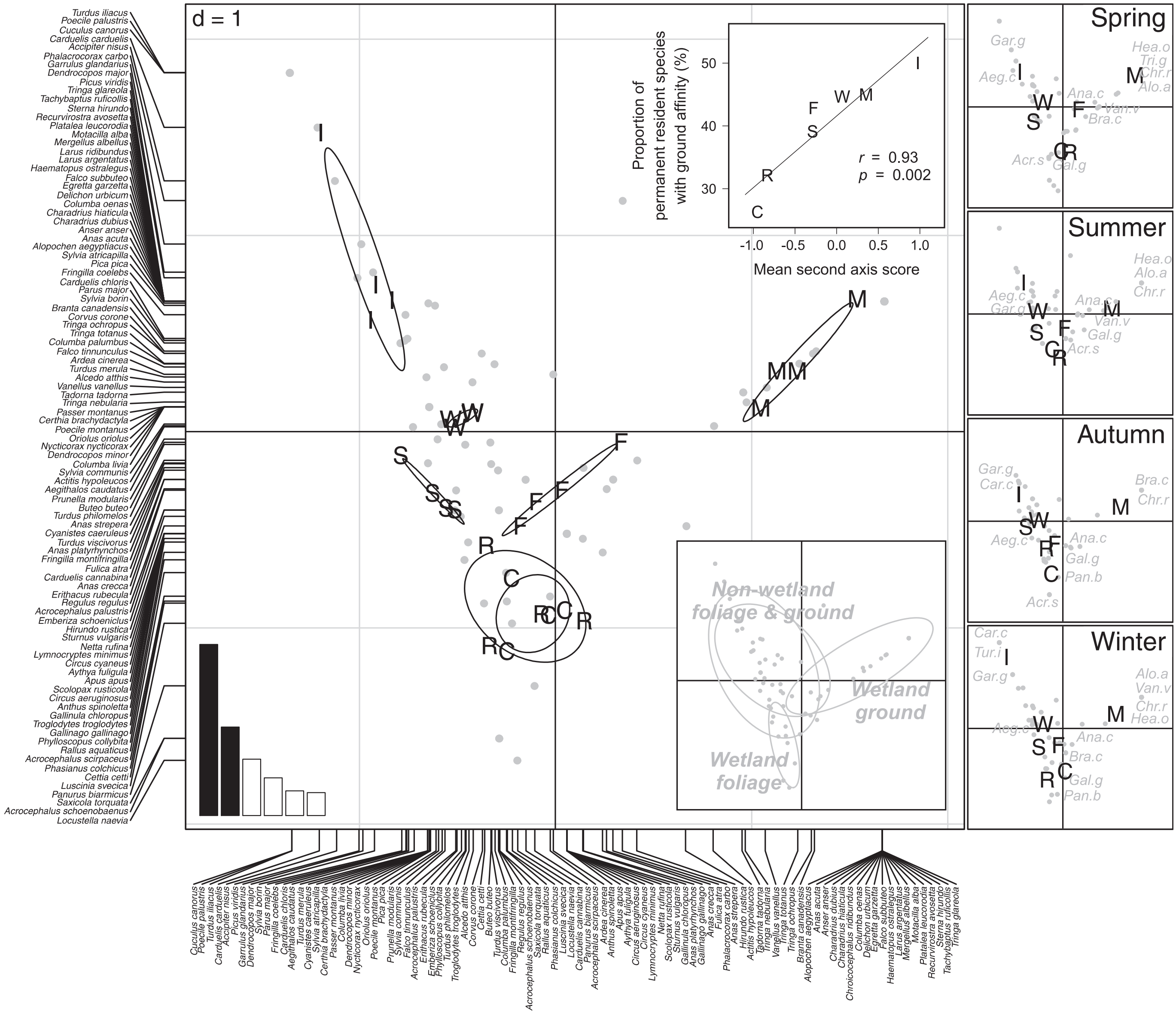

Fig. 4. Foucart's correspondence analysis (FCA). Bottom-left corner, eigenvalue diagram: axis 1 (horizontal), 43%; axis 2 (vertical), 22%. Left panel: average positions of species (grey points, labels positioned on bottom and left sides); seasons (black characters), are grouped per habitat; "*d*" indicates the grid scale; lower insert, species grouped per ecological groups; upper insert, relationship between mean habitat second axis score and proportion of permanent resident species with an affinity for ground (G and FG groups); mean habitat position (ellipse gravity centre) is obtain from the reference matrix (see method). Right panels: respective seasonal positions of species (grey points) and habitats (black characters) deviating from the reference position; each panel represent the pattern of habitats at the given season. Abbreviations of the most contributing species (see Table A.3 for absolute contributions): *Aeg.c*, *Aegithalos caudatus*; *Acr.s*, *Acrocephalus scirpaceus*; *Alo.a*, *Alopochen aegyptiacus*; *Ana.c*, *Anas crecca*; *Bra.c*, *Branta canadensis*; *Car.c*, *Carduelis carduelis*; *Gar.g*, *Garrulus glandarius*; *Hae.o*, *Haematopus ostralegus*; *Chr.r*, *Chroicocephalus ridibendus*; *Pan.b*, *Panurus biarmicus*; *Tri.g*, *Tringa glareola*; *Tur.i*, *Turdus iliacus*; *Van.v*, *Vanellus vanellus*.

the two species pools, indicating that the habitats created by a CRT are representative for freshwater tidal marsh ecosystems.

4.2. Spatiotemporal community structure

Univariate and multivariate approaches brought complementary evidence of non-random habitat occupancy by species along the habitat gradient created by the CRT. This is a typical feature of bird communities in natural ecosystems (MacArthur, 1964; Block and Brennan, 1993), and particularly along gradients of vegetation types as in the present case (Adams, 1908; MacArthur and MacArthur, 1961; Blondel, 1973; Willson, 1974). Most habitats were characterized by distinct bird communities, although the Forbs habitat was characterized by both typical wetland bird species as terrestrial bird species. In this habitat, ecological groups intersected (Fig. 4, lower insert), which explains the highest number of species encountered in this habitat. This also agrees with Weller (1973) who suggested that increased tidal freshwater habitat use by birds is promoted by plant community diversity as it is the case in Forbs. Whereas bird species richness can exhibit increasing tendencies in terrestrial gradients (May, 1982), no clear pattern arose here. This suggests that, along the gradient, no habitat offers a common environmental optimum to a majority of species. From helophytes to woody plants, foliage complexity may explain this pattern since it was shown to increase species richness (MacArthur and MacArthur, 1961); among the foliated habitats, species richness was minimal in Reed and Cattail, which offer more uniform foliages.

The spatial pattern highlighted by FCA confirmed the hypothesized habitat community specificity along the environmental gradient, and brings two important remarks. Firstly, the configuration of habitat ordination remained fairly unchanged across seasons; this shows that between-habitat differences in resource availability remain constant from spring to winter. Secondly, the stable amplitude of the configuration across seasons indicates that the number of shared species between habitats remained relatively constant (Table A.4), otherwise a decrease or increase in amplitude would have revealed either community homogenization (increase of taxonomic similarity, closer habitat positions) or community differentiation (decrease of taxonomic similarity, more distant habitat positions). These results point to a strong habitat community specificity and a stable diversity of associations between CRT habitats and bird species despite some marked seasonal species turnovers (Table A.2). This contrasts with bird communities from non-tidal wetlands where community structure varies depending on seasonal water fluctuations (Elmberg et al., 1993; Froneman et al., 2001; Gonzáles-Gajardo et al., 2009). Here, the constant flooding frequency induced by the tide may sustain water dependant resources so that habitats are maintained in all seasons. In such a case, CRT could locally benefit a large diversity of wetland bird species by compensating the loss or impairment of non-tidal wetland habitats.

Given the strong migratory nature of half of the species present, seasonal effects on community structure were obvious in all habitats, unlike year effect, generally encountered in restoration processes. The rapid habitat development during the year preceding the bird monitoring (Jacobs et al., 2009) probably explains the weakness or the absence of a year effect on community structure in all habitats. As displayed by Fig. 2, most species were already present the first monitoring year, particularly in the richest and the most populated habitats. In restored intertidal habitats through managed realignment in the UK, the main community changes were shown to occur within the first year (Atkinson et al., 2004; Mander et al., 2007). Generally, once habitats are created, benthic invertebrates and birds respond fairly quickly if conditions are suitable (Atkinson, 2003; Ma et al., 2004). Habitat quality is mostly the leading criterion to ensure a successful restoration for foraging waterfowls (Atkinson, 2003; West et al., 2005). Indeed, sediment characteristics play a key-role since they condition prey densities, and particle size distribution was shown to be a relevant predictor of shorebirds densities (Yates et al., 1993). In the CRT, the lowest locations from which Mudflat, Cattail and Reed habitats developed received 15 cm of silty estuarine sediment after less than one year (Vandenbruwaene et al., 2011); higher macroinvertebrate densities were found compared to those encountered on the adjacent estuarine sandflats (Beauchard et al., 2013). This may explain the absence or the weakness of year effect on community structure, at least in Mudflat, dominated by benthivorous birds.

However, at the species scale, the abundances of three species of the most frequent ones exhibited inter-annual increases (Fig. A.1), requiring either one year (*Anas crecca*) or more (*Emberiza schoeniclus*, *Acrocephalus scirpaceus*) to become stable over several years. Positive covariations occurred between abundances and the amount of specific resources emerging from CRT habitats: *A. crecca*, a wintering bird in the Schelde estuary, feeding on tubificids on estuarine flats (Ysebaert et al., 2000), with winter tubificid densities; *A. scirpaceus*, a reed specialist, with Reed coverage, and probably explaining the slightly significant year effect on Reed community; massive populations of *E. schoeniclus* were observed to forage in Loosestrife foliage when seeds reached maturation. This points to successful habitat uses by migratory species for overwintering or breeding (*A. scirpaceus*; see below).

4.3. Tidal effect

The tide effect was more substantial on the Forbs and Mudflat communities. Three characteristic benthivores, among the most frequent species in both the CRT and the adjacent tidal flats where they forage at low tide (Ysebaert et al., 2000), *Anas crecca*, *Anas platyrhynchos* and *Anas strepera*, were the most sensitive ones to the tidal effect (Fig. A.2). In estuaries, waterbird behaviour and movements are generally regulated by the tidal cycle, during which birds use terrestrial resting grounds (roots) or foraging grounds at high tide (Rogers, 2003; Shepherd et al., 2003; Burton et al., 2004). As a consequence of the CRT system, the polder is flooded with a delay of nearly 1.5 h compared to the adjacent river tidal flats (Beauchard et al., 2011); moreover, almost no water enters the polder at neap tide. Hence, CRT offers extended feeding time for species that also forage on the adjacent tidal flats, especially when large areas are created. This may explain the tide effect on Forbs and Mudflat communities when the adjacent river flats were submerged at high tide and thus unavailable for birds, as already shown in wetlands adjacent to an estuary (Davidson and Evans, 1986; Evans et al., 1998). This hypothesis was rejected since abundances were not determined by the availability of the adjacent flats (Table A.5, Fig. A.2).

4.4. Additional remarks on breeding

Dabbling duck nests (*Anas platyrhynchos* and *Anas strepera*) were observed every year in Forbs, but they were either abandoned during building or after spring tide events. Although this aspect is also poorly documented for dabbling ducks, the tidal cycle may have acted as an ecological trap for these species, as already observed for other species in North America (Gjerdrum et al., 2005; Nordby et al., 2009). Contrary to the statements of Barendregt et al. (2009), breeding below the mean high water level was possible; *Fulica atra* and *Gallinula chloropus* built floating nests to cope successfully with inundation. In addition, successful breeding was observed for several species: *Acrocephalus palustris*, *Acrocephalus scirpaceus*, *Alcedo atthis*, *F. atra*, *G. chloropus* and *Sylvia communis*. The CRT also ensured a nursery function as chicks, mainly from ducks, were regularly observed feeding.

4.5. A positive avian response to CRT habitat creation?

This study assessed the suitability of an area equipped with a CRT system to marsh bird communities. The CRT generated a typical freshwater tidal gradient from bare mudflat to different types of marsh vegetation, together with some remnant terrestrial vegetation. This clearly shows that the different ecological groups of species were coherently distributed among habitats and were not significantly disproportionate than those encountered in the species pool derived from regional tidal freshwater wetlands. Moreover, the high diversity of species, among which one third exhibits conservational importance or concern at local and/or international scale, adds a strong conservation value to CRT habitats. Hence, these findings indicate a positive avian response relative to the experimental context and, given the limited spatial extend of this study, they may express a higher potential when implementing CRT over larger surface areas. The CRT system is therefore a promising way to restore estuarine freshwater tidal habitats, and at the same time provide safety against flooding.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2013.06.026.

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