

# Ecological recovery in an Arctic delta following widespread saline incursion

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**Abstract.** Arctic ecosystems are vulnerable to the combined effects of climate change and a range of other anthropogenic perturbations. Predicting the cumulative impact of these stressors requires an improved understanding of the factors affecting ecological resilience. In September of 1999, a severe storm surge in the Mackenzie Delta flooded alluvial surfaces up to 30 km inland from the coast with saline waters, driving environmental impacts unprecedented in the last millennium. In this study we combined field monitoring of permanent sampling plots with an analysis of the Landsat archive (1986–2011) to explore the factors affecting the recovery of ecosystems to this disturbance. Soil salinization following the 1999 storm caused the abrupt dieback of more than 30 000 ha of tundra vegetation. Vegetation cover and soil chemistry show that recovery is occurring, but the rate and spatial extent are strongly dependent on vegetation type, with graminoid- and upright shrub-dominated areas showing recovery after a decade, but dwarf shrub tundra exhibiting little to no recovery over this period. Our analyses suggest that recovery from salinization has been strongly influenced by vegetation type and the frequency of freshwater flooding following the storm. With increased ocean storm activity, rising sea levels, and reduced sea ice cover, Arctic coastal ecosystems will be more likely to experience similar disturbances in the future, highlighting the importance of combining field sampling with regional-scale remote sensing in efforts to detect, understand, and anticipate environmental change.

**Key words:** climate change; disturbance; ecosystem recovery; Mackenzie Delta; resilience; saline incursion; storm surge.

## INTRODUCTION

The cumulative impacts of global climate change and anthropogenic disturbance will dramatically alter coastal ecosystems. Model projections indicate that coastal areas will be subjected to more intense storm activity and rising sea levels (Scavia et al. 2002, IPCC 2007, Knutson et al. 2010). These changes will increase coastal inundation and erosion, alter vegetation structure, productivity, and composition, and impact ecosystem function and biodiversity (Gornish and Miller 2010, Howes et al. 2010, Byrnes et al. 2011, Torresan et al. 2012, Tate and Battaglia 2013). In most cases, these changes will occur in ecosystems where anthropogenic stressors (nutrient loading, overfishing, oil spills, etc.) are already driving shifts in ecosystem structure, feedbacks, and functioning (Viaroli et al. 2008, Mollmann et al. 2009, Silliman et al. 2012). With rapid declines in sea-ice cover, rising sea level, and increased storm intensity, Arctic coastlands are likely to be particularly susceptible to more frequent saline incursions.

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sion (Walker 1998, IPCC 2007, Comiso et al. 2008, Sepp and Jaagus 2011). To inform planning in Arctic communities and protected areas and guide decision making related to existing and proposed industrial infrastructure, an improved understanding of ecosystem recovery following saline inundation is required. In this paper we examine ecological recovery in the Mackenzie Delta following a storm surge that impacted tundra communities >30 km inland, and discuss the implications for northern planning.

The Mackenzie Delta is a low-lying alluvial plain intersected by a network of channels and thousands of small lakes (Mackay 1963, Burn and Kokelj 2009; also see Fig. 1). The delta is comprised of sediments deposited by the Peel and Mackenzie Rivers, which drain approximately one-fifth of Canada's land mass (Mackay 1963). The Mackenzie Delta provides critical habitat to resident and migratory fish, waterfowl, and mammals (Bromley and Fehr 2002, Nagy 2002, Stephenson 2002). The Mackenzie Delta is also part of the homeland of both the Inuvialuit and Gwich'in peoples, and is an area critical for harvesting subsistence foods (Wein and Freeman 1995, Usher 2002, Thompson and Millar 2007).

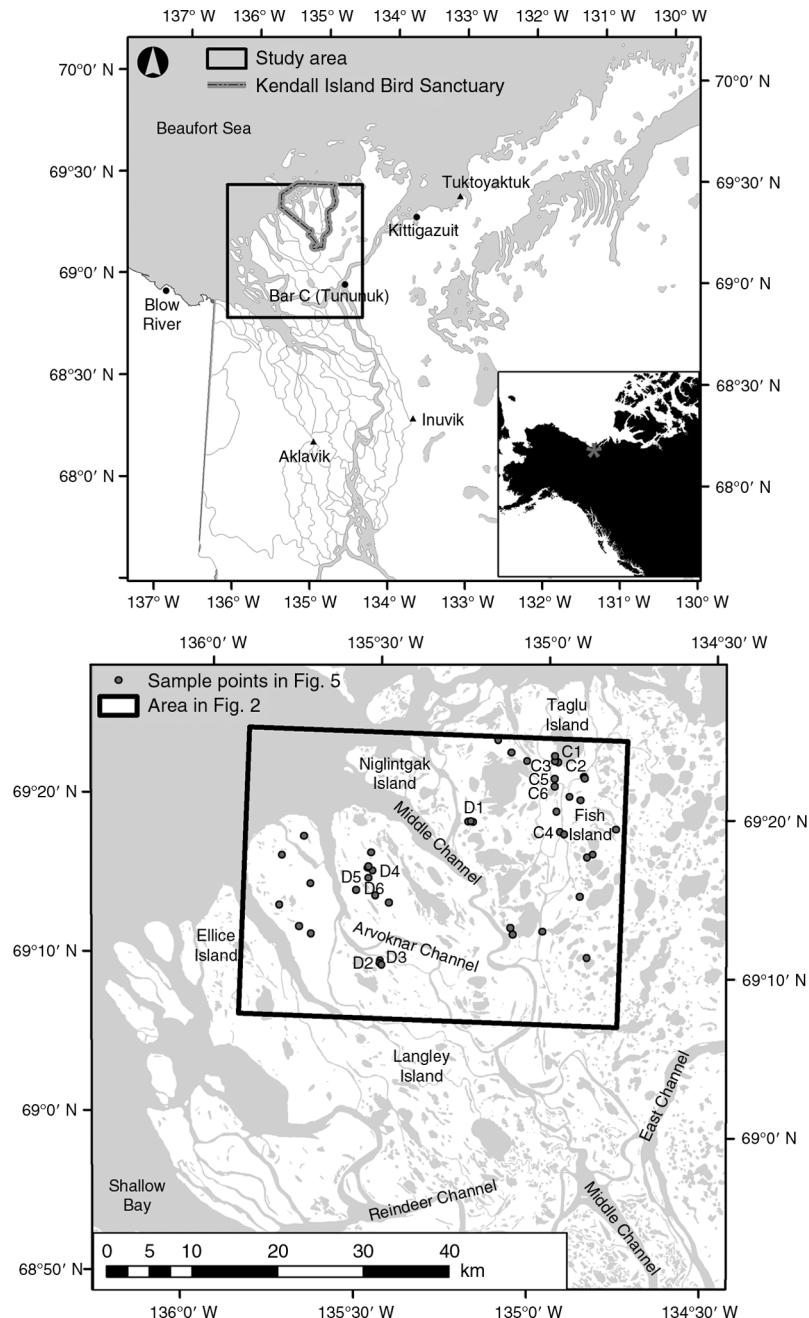


FIG. 1. Map of the study area. The upper panel shows the location of study area (solid black box) and the Kendall Island Bird Sanctuary (dashed line) within the Mackenzie Delta region. The asterisk on the inset map at the bottom right shows this area in western North America. The lower panel shows the location of impacted (D1–D6) and unimpacted (C1–C6) sampling sites, the area displayed in Fig. 2, and the location of the polygons used in the Normalized Difference Vegetation Index (NDVI) analysis (Fig. 5).

In September of 1999, a severe storm surge in the Mackenzie Delta region flooded alluvial surfaces up to 30 km inland from the coast with highly saline waters. Synthetic aperture radar and hydrometric data indicate that all terrestrial surfaces in the outer delta were completely inundated for a period of several days (Kokelj et al. 2012). Following the storm, large areas

of terrestrial vegetation died back (Appendices A–C), and have shown limited recovery (Fig. 2 [Kokelj et al. 2012]). Ecological recovery in several closed-system lakes has also been extremely limited (Thienpont et al. 2012). Sediment cores obtained from surge-impacted lakes in the outer delta showed a rapid change in algal community composition following the storm, shifting

from dominance by freshwater to marine species. Combined with the absence of marine diatoms in unimpacted lakes, these data show that saline inundation of this magnitude has no analog in the last millennium (Pisaric et al. 2011, Thienpont et al. 2012). Other sources of information about past conditions (alder growth rings, geochemistry of permafrost profiles, and the traditional knowledge of Inuvialuit hunters) provide additional evidence that saline incursion of this magnitude has not been common in the region (Kokelj et al. 2012).

Tracking recovery in the outer delta is critically important for Inuvialuit land-users and regional land-use planners, and provides a unique opportunity to explore the factors influencing ecological recovery from a novel form of disturbance that is likely to become more common in the Arctic (IPCC 2007, Comiso et al. 2008, Goulding et al. 2009, Knutson et al. 2010). In this paper we examine the factors influencing the recovery of terrestrial ecosystems following the 1999 storm surge by tracking ecological trajectories in three vegetation types (graminoid, upright shrub, and dwarf shrub) at two spatial scales.

## METHODS

### *Study sites*

The Mackenzie Delta is a dynamic environment, underlain by continuous permafrost and shaped by frequent ice jam flooding (Goulding et al. 2009, Nguyen et al. 2009). This paper focuses on the low-lying (<2 m) northern portion of the Mackenzie Delta and is referred to throughout the paper as the outer delta (Fig. 1). Ecosystems in the outer delta are shaped by the frequency, duration, and timing of flooding, which influences sedimentation, soil moisture, soil chemistry, permafrost conditions, and limits vegetation succession (Mackay 1963, Marsh and Schmidt 1993, Johnstone and Kokelj 2008, Morse et al. 2009). In this paper we examined recovery following the 1999 storm in terrain types defined using the structure of the dominant vegetation. Throughout this paper these terrain types are referred to as: graminoid, upright shrub, and dwarf shrub (Appendix A). Graminoid sites occur on poorly drained, low-elevation inter-levee basins. These areas are typically flooded annually for 5–100 days and are dominated by *Carex aquatilis* Wahlenb and *Eriophorum angustifolium* Honck (Cordes et al. 1984, Pearce 1986). Sites dominated by upright shrubs occur on slightly elevated surfaces adjacent to channels and lakes. This vegetation type is characterized by a mix of Richardson's and felt-leaf willows (*S. lanata* subsp. *richardsonii* (Hook.) Skvortsov and *Salix alaxensis* (Anderss.) Cov.)

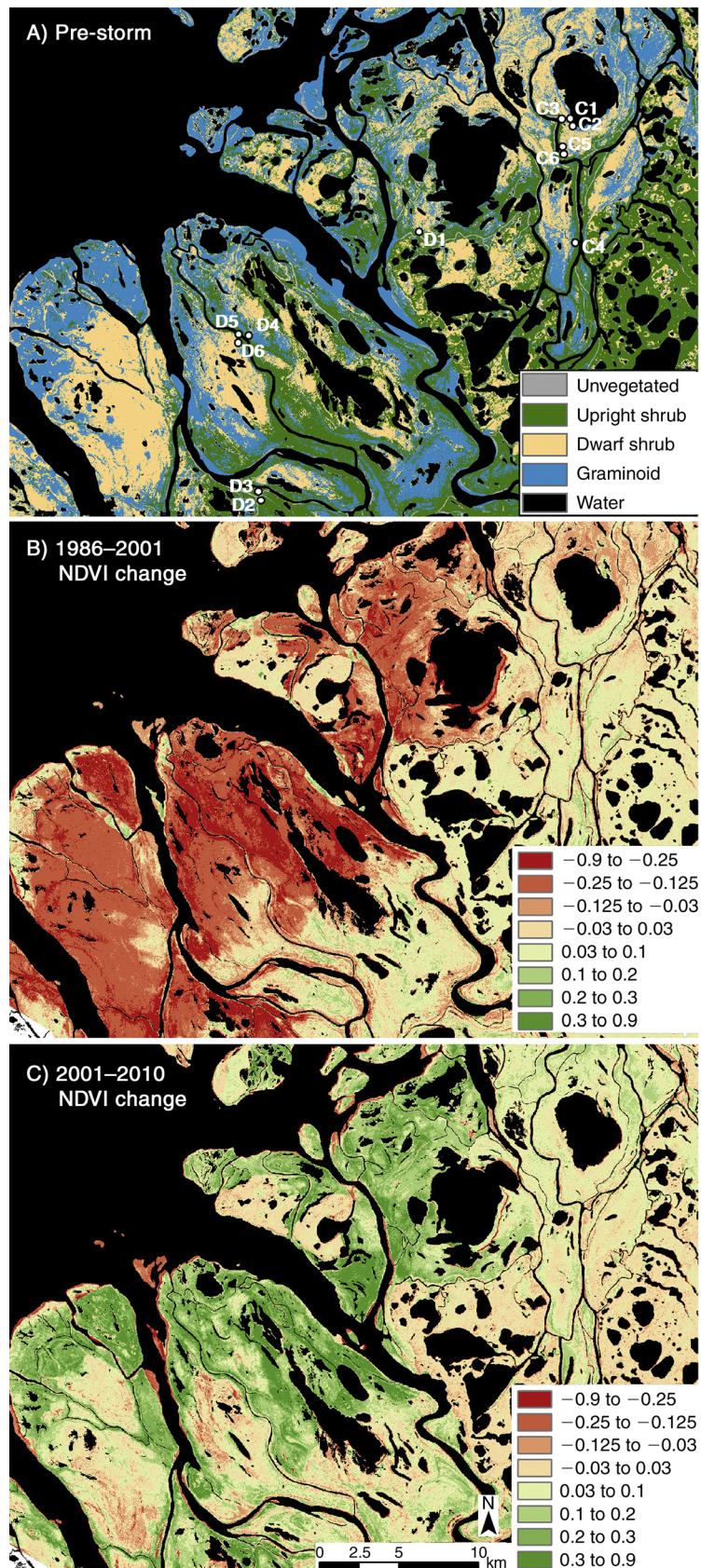
with an understory of *Carex aquatilis*, moss and sparse cover of *Equisetum arvense* L. and *Hedysarum alpinum* L. The flood return interval at upright shrub-dominated sites is variable, ranging from annual to decadal. Regardless, flooding of these sites typically lasts no more than a few days (Cordes et al. 1984, Pearce 1986). The most elevated surfaces in outer delta are host to dwarf shrub communities. This vegetation type is infrequently affected by spring flooding (less frequently than every 10 years), and when it is, inundation is brief (1–2 days). Vegetation at dwarf shrub sites is dominated by *Arctostaphylos rubra* (Rehd. & Wils.), *Dryas integrifolia* M Vahl., and Richardson's willow (Cordes et al. 1984, Pearce 1986, Kemper and Macdonald 2009).

To examine the effects of the storm on biotic and abiotic parameters, we established 12 long-term monitoring transects in 2007; 6 transects were located in impacted portions of the study area, and 6 transects were set up in areas negligibly impacted by the 1999 storm (Kokelj et al. 2012). Transects were established perpendicular to the nearest channel so that they traversed the three vegetation types just described. To ensure that all vegetation types were well represented, transect lengths were set at either 100 or 200 m, with 11 sample points located at 10- or 20-m intervals, respectively (Appendices B and C). To mark the locations of each transect we anchored plot markers (rebar rods fitted with plastic sleeves) into near-surface permafrost. Nearshore areas in proximity to the delta are strongly influenced by the freshwater plume of the Mackenzie River, and terrestrial salinity gradients are generally weak (Carmack and MacDonald 2002, Kokelj et al. 2009, 2012). Since our sites were all >10 km from the ocean, it is unlikely that the vegetation was strongly influenced by salinity before the storm (Gill 1971, Cordes et al. 1984, Pearce 1986, Morse et al. 2009). To examine recent changes in biotic and abiotic parameters at impacted and unimpacted sites, in August, 2010 we returned to each permanently marked transect and repeated the measurements described below.

### *Soils, vegetation, and hydrology*

Along each transect, we visually estimated the percentage cover of all vascular plants inside quadrats positioned around each sampling point ( $n=11$ ). Upright shrub cover (willow and alder) was estimated using a  $2.24 \times 2.24$  m quadrat at each sampling plot. The percentage cover of all other vascular plants, as well as bryophytes and lichens, was estimated using two  $0.5 \times 0.5$  m quadrats nested inside the  $2.24 \times 2.24$  m quadrat. Nomenclature for vascular plants follows Porsild and Cody (1980) and Catling et al. (2008).

FIG. 2. Maps showing vegetation structure and regional changes in NDVI. (A) Supervised classification of a pre-storm Landsat scene (24 July 1998) showing the distribution of major terrain units. (B) NDVI change between 1986 and 2001. The large red areas show areas of vegetation killed by the 1999 storm surge. (C) NDVI change between 2001 and 2010. Impacted areas that have shown significant recovery appear green, and impacted areas that have shown little recovery appear as pale yellow.



A suite of abiotic parameters was also measured along each transect. Active-layer thickness was determined at each sample point by pushing a calibrated steel probe to depth of refusal. The thickness of the organic layer (well to partly decomposed organic matter, excluding undecomposed surface litter) was measured at each point using a small metal ruler. Composite soil samples were collected at each point using a gouge auger. Soil samples were bagged and stored in a cool dark place, and then returned to the laboratory for analysis. Soil samples were evaluated for gravimetric moisture content, pH, electrical conductivity of soil pore water (EC) and soluble ions, following (McKeague 1978). To record the elevation of sampling points, we used a Trimble R3 Differential GPS system with Pro XT receivers connected to Ranger field computers.

To assess the frequency, magnitude, and duration of flooding in the outer delta following the 1999 surge, we obtained stage data from Reindeer Channel at Ellice Island (Water Survey of Canada gauge 10MC011). Data corrected to the Canadian Gravimetric Geoid (CGG) 2005 vertical datum by the National Hydrology Research Institute (M. Russell, Environment Canada, *personal communication*) were used to calculate the number and duration of events where the gauge exceeded 1 and 2 m above the mean river level (0.92 m).

#### *Remote sensing analysis*

To investigate vegetation changes at a broader scale than our permanent sampling plots, we used archived TM and ETM+ imagery from the Landsat 5 and 7 satellites. Thirteen Landsat images (30 m resolution) from three overlapping Worldwide Reference System-2 frames were obtained from the USGS Global Visualization Viewer (GloVis) system.<sup>5</sup> All but one of these images (2000) provided >90% cloud-free coverage of a 1400 km<sup>2</sup> study area (Fig. 1: lower inset) and spanned growing-season acquisition dates between 10 July and 19 August 1986–2011. Landsat scenes were calibrated to radiance using coefficients provided by USGS (Chander et al. 2009), then converted to top-of-atmosphere reflectance. Images were manually masked for cloud within the study areas, and spatial data gaps in the SLC-off Landsat-7 image from 2000 were treated as cloud / no-data. The Normalized Difference Vegetation Index (NDVI), measuring the contrast between near-infrared and red reflectance (Tucker 1979), was computed for each image to provide a measure of green vegetation leaf area and phytomass (Riedel et al. 2005, Raynolds et al. 2012).

To assess NDVI dynamics in each vegetation type (upright shrub, dwarf shrub, and graminoid) in the impacted and unimpacted part of the study area, we manually delineated 6–8 polygons in each of the six site types using color orthophotos (2004) and low-altitude

oblique photographs (2009 and 2010). Polygons ( $n=48$ ) covered a total area of ~400 ha. Mean NDVI was calculated for each year and site type, and plotted to examine trends in vegetation recovery following the 1999 storm. To estimate the area of vegetation impacted by the storm surge, we used a threshold value of NDVI change between 1986 and 2001 to create an image mask. We used a threshold of -0.1 NDVI because this exceeds three standard deviations of the mean interannual variation in NDVI at unimpacted sites (0.089). This value also captured almost all of the visibly affected areas while producing minimal commission error outside of the surge zone. This annual analysis extends previous work (Kokelj et al. 2012) which contrasted NDVI in this region using two Landsat images (1986 and 2005).

#### *Statistical analysis*

To explore differences in plant community composition among impacted and unimpacted vegetation types in 2007 and 2010 we used PRIMER to perform nonmetric multidimensional scaling (NMDS) ordinations (Clarke and Gorley 2001). This analysis was conducted using Bray–Curtis distance matrices calculated from two data sets: (1) percentage cover of species at all unimpacted sites (2007 and 2010), and (2) percentage cover of species at all impacted and unimpacted sites (2007 and 2010). In both cases we set PRIMER to repeat the analysis 20 times and selected the best two-dimensional representation of the original distance matrix (i.e., least stress) (Legendre and Legendre 1998). To reduce noise and stress we use a  $\log_{10}(1+x)$  transformation of percentage cover data. Subsequently, we used ANOSIM (Analysis of Similarities) to test the null hypothesis that species composition did not differ among site types (combinations of impacted, unimpacted, vegetation type, and year).

To identify the species making the largest contribution to: (1) the compositional similarities of a given vegetation type, and (2) the dissimilarities among vegetation types, we used the SIMPER function in PRIMER to calculate the percentage contribution of each species to the Bray–Curtis dissimilarities among site types (Clarke and Gorley 2001). Since community composition at unimpacted sites was effectively indistinguishable in 2007 and 2010 (Table 1), we simplified the ordinations shown in Fig. 3 by grouping unimpacted sites across years. To examine correlations between community structure and the abiotic parameters measured in each plot, we used the ENVFIT function in the VEGAN package for R. The significance of these correlations was assessed using 9999 random permutations of the data (R Development Core Team 2006).

To test for significant differences in biotic and abiotic response variables between impacted and unimpacted areas, and among vegetation types and years, we used linear mixed effects models (PROC MIXED; SAS 2004). In our models we treated impact, vegetation type, and year as fixed effects and transect as a random

<sup>5</sup> <http://glovis.usgs.gov>

TABLE 1. Pairwise comparisons of plant community composition among vegetation types at impacted and unimpacted sites in the outer delta using the ANOSIM procedure.

Impact	Date	Type	Impacted						Unimpacted					
			2007			2010			2010			2007		
			US	G	DS	US	G	DS	US	G	DS	US	G	
Unimpacted	2007	DS	0.29	<b>0.69</b>	<b>1.0</b>	0.03	<b>0.59</b>	<b>0.95</b>	0.26	0.33	0.06	0.19	0.35	
		G	<b>0.50</b>	<b>0.55</b>	<b>0.99</b>	0.35	<b>0.43</b>	<b>0.96</b>	0.27	0.02	0.32	0.23		
		US	0.33	<b>0.55</b>	<b>0.96</b>	0.09	<b>0.45</b>	<b>0.88</b>	0.01	0.21	0.122			
	2010	DS	0.27	<b>0.65</b>	<b>1.0</b>	0.01	<b>0.52</b>	<b>0.94</b>	0.18	0.28				
		G	<b>0.47</b>	<b>0.48</b>	<b>0.99</b>	0.31	0.34	<b>0.96</b>	0.21					
		US	0.26	0.39	<b>0.89</b>	0.07	0.36	<b>0.81</b>						
Impacted	2010	DS	0.01	<b>0.52</b>	0.22	0.22		<b>0.78</b>						
		G	<b>0.43</b>	0.16	0.22	0.22								
		US	0.09	0.15										

Notes: Vegetation types are abbreviated as: dwarf shrub (DS), graminoid (G), and upright shrub (US). Comparisons are based on a Bray-Curtis distance matrix. Values of  $R_{ANOSIM} > 0.75$  indicate that site types are well separated; values between 0.5 and 0.75 describe overlapping but distinguishable groups; and values < 0.25 are characteristic of groups that can barely be separated.  $P < 0.01$  for all comparisons shown in boldface type ( $R_{ANOSIM} > 0.4$ ).

effect. In all of our models we assumed a simple covariance structure by using the variance components option for random effects. To estimate the error degrees of freedom for all  $F$  tests of fixed effects we used the Kenward–Roger approximation (SAS 2004). When interactions among fixed effects were present, we conducted Tukey adjusted pairwise comparisons using the LSMEANS procedure (SAS 2004, Littell 2006). To meet the assumptions of normality and equal variance, the following response variables were log transformed: pore-water electrical conductivity (EC), soil chloride, soil moisture, shrub cover, moss cover, graminoid cover, and total vegetation cover.

## RESULTS

### Plant community composition: unimpacted sites

Multivariate analysis of vegetation cover revealed considerable overlap in species composition among classes defined based on vegetation structure (Fig. 3A; Appendix D: Table D1;  $R_{ANOSIM} = 0.01\text{--}0.35$ ). Despite observed overlap, a large portion of the similarity (>40%) within a given vegetation type could be attributed to the abundance of a single species or group (Table 2). Graminoid sites were characterized by an abundance of *Carex aquatilis*; dwarf shrub sites had an abundance of moss; and upright shrub sites were dominated by *Salix lanata* subsp. *richardsonii* (Table 2). Community composition at undisturbed sites was significantly correlated with abiotic variation in the outer delta. Graminoid sites were associated with thick organic layers, high soil moisture, lower elevation, and thinner active layers. Dwarf shrub sites tended to have thick organic layers and higher soil moisture, and low pH. Community composition at upright shrub sites was correlated with high pH, thick active layers, and higher elevation (Fig. 3A). There was no evidence of changes in community composition at unimpacted sites between 2007 and 2010 ( $R_{ANOSIM} \leq 0.06$ ; Table 1).

### Plant community composition: impacted sites

The multivariate analysis of vegetation in the outer Mackenzie Delta shows that the 1999 storm surge had significant effects on community composition in all vegetation types. Differences in plant community composition between impacted and unimpacted sites were significantly correlated with elevated soil chloride, sodium, and magnesium, reduced moisture, and increased electrical conductivity (Fig. 3B). The magnitude of differences in community composition between impacted and unimpacted sites depended strongly on vegetation type (Fig. 3B, Table 1). The largest and most persistent differences in community composition between impacted and unimpacted sites were observed at dwarf shrub sites (Fig. 3, Table 1). ANOSIM comparisons showed that impacted and unimpacted dwarf shrub sites were almost completely dissimilar in both 2007 and 2010 ( $R_{ANOSIM} = 0.94\text{--}1.0$ ). This difference was driven by an abundance of dead willow, and decreased cover of moss, *Equisetum variegatum*, and Richardson's willow at impacted sites (Appendix D). Graminoid sites were also significantly altered by the 1999 storm surge. Impacted graminoid sites were totally distinct from undisturbed sites in 2007 (Fig. 3B, Table 1;  $R_{ANOSIM} = 0.69$ ). Differences between these site types were driven by an increase in the cover of dead willow, and lower cover of *Carex aquatilis* and moss at impacted sites (Appendix D). By 2010, the differences in community composition at impacted and unimpacted graminoid sites were less pronounced ( $R_{ANOSIM} = 0.34$ ), indicating gradual ongoing recovery of this vegetation type. Upright shrub sites were the least impacted vegetation type, showing greater similarity between impacted and unimpacted community composition than any other vegetation type. In 2007, community composition at impacted upright shrub sites was only marginally different than unimpacted sites (Fig. 3, Table 1;  $R_{ANOSIM} = 0.33$ ). Compositional dissimilarity between these sites was driven by the dominance of dead

willow and reduced cover of living willow, *Carex aquatilis*, and moss at impacted sites (Appendix D). By 2010, upright shrub sites had shown extensive recovery, and community composition at impacted and unimpacted upright shrub sites could not be distinguished (Table 1;  $R_{ANOSIM} = 0.07$ ).

#### *Vegetation cover*

The severe impact of the 1999 storm surge on vegetation was evident 8 and 11 years following the storm (Fig. 2). The magnitude of these effects depended on the vegetation type and plant functional group (Fig. 4). Total vegetation cover was lower in impacted areas compared with unimpacted areas, and these differences were significant at dwarf shrub (2007 and 2010) and upright shrub (2007) dominated sites (Fig. 4A). The cover of graminoid and woody vegetation was also lower at impacted vs. unimpacted sites, but significant differences were restricted to upright shrubs and dwarf shrubs (Fig. 4B, C). Severe and persistent reductions in moss cover were observed across all vegetation types (Fig. 4D).

Recovery following the storm was extremely limited in areas of dwarf shrub tundra. These sites were virtually devoid of all vegetation in 2007 (Fig. 4). Impacted dwarf shrub sites showed a small (~10%), but significant, increase in total vegetation cover between 2007 and 2010. These changes were the result of the establishment of several species: *Melandrium apetalum* (L.) Fenzl, *Festuca rubra* subsp. *Richardsonii* (Hook) Hultén, *Hedysarum alpinum* L., and *Equisetum variegatum* Schleich. Small increases were also observed in all functional groups, but they were not significant (Fig. 4B–D). Despite these changes, total vegetation cover at dwarf shrub sites in 2010 remained significantly lower than unimpacted areas (Fig. 4A). At unimpacted sites the cover of all functional groups did not change between years (Fig. 4).

#### *Changes in NDVI (1986–2011)*

Our analysis of the Landsat archive shows that ~31 204 ha of vegetation in the outer delta study area was impacted by the saline incursion in 1999. These estimates are considerably larger than those by Kokelj et al. (2012), because we used a smaller threshold to define the impacted area and had a larger archive of imagery that could more effectively estimate impacts following the storm. The largest changes in NDVI occurred in the area southwest of Middle Channel, where most land surfaces showed reductions in  $NDVI > 0.1$  (Fig. 2). On Niglintgak Island and in the Kendall Island Bird Sanctuary, reductions in NDVI were limited to low-lying alluvial areas, and non-alluvial uplands showed no change (Fig. 2). Comparisons of average NDVI over time show that widespread vegetation dieback occurred within the first two years after the storm (Fig. 5). At graminoid sites the lowest observed NDVI levels occurred one year following the storm, but in upright

and dwarf shrub sites NDVI continued to decline until 2001 (Fig. 5).

The Landsat NDVI time series also shows that significant, but patchy, recovery has occurred in most parts of the outer delta (Fig. 2). Widespread recovery did not begin until after 2005, but by 2011, roughly two-thirds of the impacted area (20 454 ha) had shown an increase in  $NDVI > 0.1$  (Fig. 2C). Changes in mean NDVI by vegetation type show that recovery has been limited primarily to graminoid and upright shrub sites (Fig. 5). Approximately 14% of the impacted area (4288 ha), including several large areas distant from major channels, have shown no net increase in NDVI since 2001 (Fig. 2). Changes in mean NDVI by vegetation type indicate that poor recovery has occurred primarily in areas previously dominated by dwarf shrub (Figs. 2C and 5).

#### *Soils*

Eleven years following the 1999 storm surge, soils in the outer delta still showed evidence of severe alteration. Impacted areas had elevated soil EC and soil chloride concentrations in all vegetation types. Soil salinity was strongly correlated with altered community composition (Fig. 3B), but the magnitude of the difference was largest at dwarf shrub sites (Fig. 6A, B). Impacted soils showed significant reductions in chloride levels and conductivity from 2007 to 2010, but the differences were only significant at upright and dwarf shrub sites (Fig. 6A, B). At un-impacted sites soil chloride and conductivity did not differ significantly among years (Fig. 6A, B). Soil moisture was significantly lower at impacted compared with un-impacted sites in all vegetation types and did not vary significantly over time at any of the vegetation types sampled (Fig. 6C). Mean active-layer thickness was significantly greater in impacted graminoid and upright shrub sites compared with un-impacted portions of these vegetation types (Fig. 6D). At dwarf shrub sites active-layer thickness was similar at impacted and un-impacted sites (Fig. 6D). In the un-impacted part of the study area active-layer thickness did not vary significantly between the two sampling periods at any of the site types (Fig. 6D).

#### DISCUSSION

The 1999 storm surge in the outer Mackenzie Delta was followed by the dieback of more than 31 000 ha of vegetation (Fig. 2). The correlation between the magnitude of observed impacts and soil chloride concentrations indicates that this change was caused by salt water inundation (Fig. 3; Kokelj et al. 2012). To our knowledge this is the only well-documented example of widespread salt kill in inland tundra vegetation not normally influenced by seawater. Saline soils limit plant growth and cause mortality by negatively affecting photosynthesis, energy metabolism, and protein synthesis (Parida and Das 2005). Salt tolerance varies considerably among species, but most plants experience

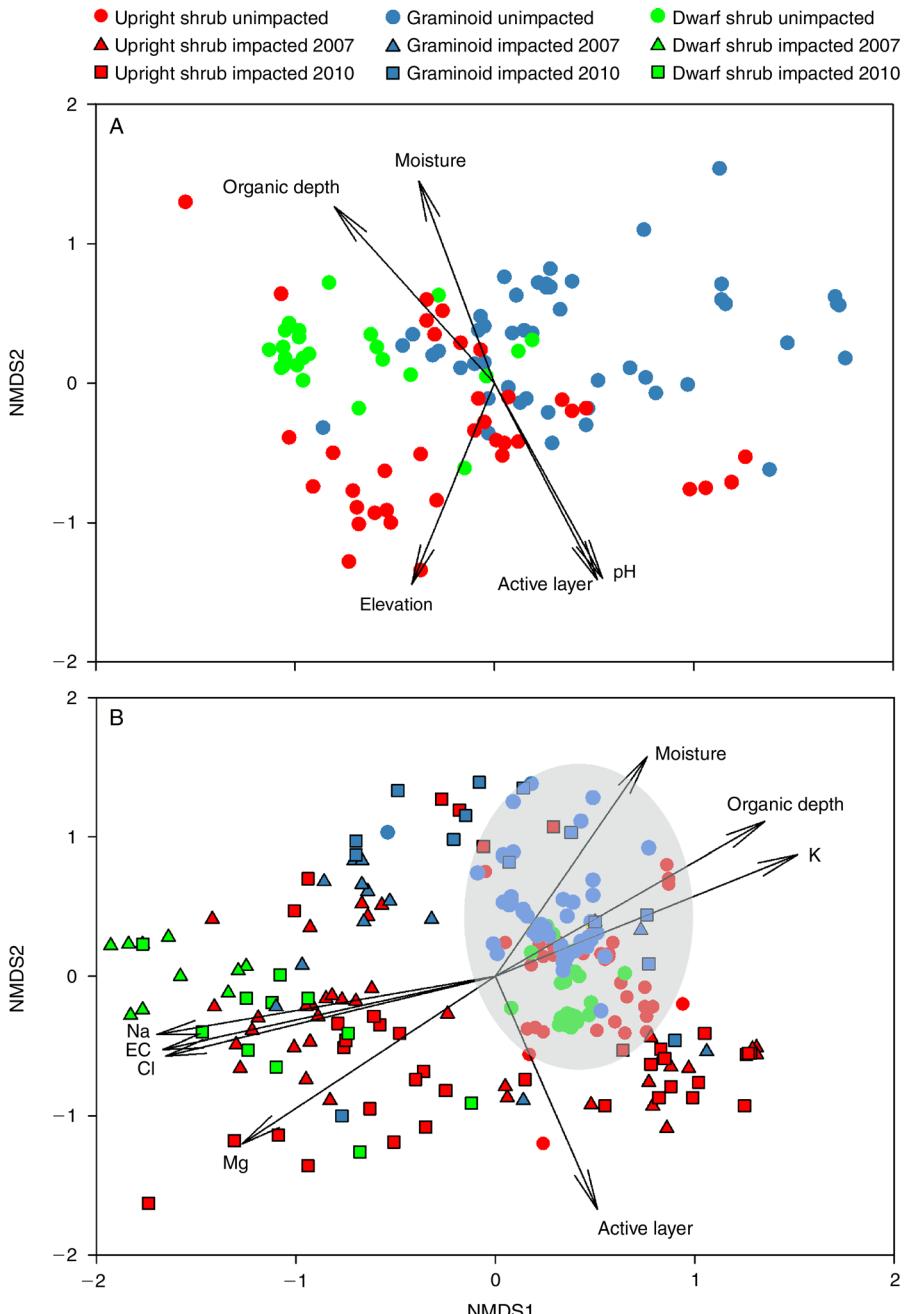


FIG. 3. Nonmetric multidimensional scaling ordination of plant community composition based on Bray-Curtis similarity matrices. The upper panel (A) shows the results of the analysis including unimpacted sites only. The lower panel (B) shows the results of an analysis including impacted and unimpacted sites. Each ordination shows the NMDS scores for each site type (colored symbols) and correlations between abiotic variables and NMDS scores (solid arrows). EC is electrical conductivity. The gray ellipse on the lower plot denotes the domain of the unimpacted sites. Unimpacted sites plotted on these ordinations include surveys from 2007 and 2010.

severe reductions in growth (>50%) at EC exceeding 4 dS/m (Earle and Kershaw 1989, Iacobelli and Jefferies 1991, Blaylock 1994). Data on salt concentrations immediately following the storm are not available, but EC measurements made in 2007 ranged from 2.8–8.8 dS/m at inland sites. Seawater has a specific conductivity of 53 dS/m (Kaye and Laby 1995), and terrestrial surfaces

in the delta were completely inundated for several days (Kokelj et al. 2012). Experimental application of seawater of at Prudhoe Bay, Alaska (2000 L/site) yielded an average conductivity of 9.2 dS/m 28 days following the storm (Simmons et al. 1983). Taken together this evidence suggests that salt concentrations in soil pore water following the 1999 storm would have

TABLE 2. Results of the SIMPER analysis characterizing similarity in community composition at undisturbed vegetation types.

Site type	Species	Mean cover (%)	Cumulative similarity (%)
Graminoid (similarity = 62.75)	<i>Carex aquatilis</i>	30.3	50.3
	moss	32.5	79.5
Dwarf shrub (similarity = 74.88)	<i>Salix lanata richardsonii</i>	17.0	93.4
	moss	65.3	41.1
	<i>Salix lanata richardsonii</i>	24.1	68.2
Upright shrub (similarity = 54.39)	<i>Equisetum variegatum</i>	16.9	93.1
	<i>Salix lanata richardsonii</i>	42.5	41.5
	moss	34.1	74.8
	<i>Carex aquatilis</i>	14.5	88.1

Notes: The top three species (or species groups) that make the greatest contribution to the between-group Bray-Curtis similarity for each vegetation type are shown. Mean cover (untransformed) of each species is shown in the third column.

exceeded 8 dS/m over large areas inundated by the 1999 storm surge. Given the late season timing of the surge (22–27 September 1999), it is likely that elevated concentrations of  $\text{Na}^+$ ,  $\text{Cl}^-$ , and  $\text{Mg}^{2+}$  would have been quickly immobilized in the freezing active layer until they became bioavailable early the following spring when the ground began to thaw. Experimental seawater application in tundra plant communities (Simmons et al. 1983), combined with information on the salt tolerance of many of the species in the outer delta (Earle and Kershaw 1989, Iacobelli and Jefferies 1991, Kincheloe

and Stehn 1991) indicate that most plants would have succumbed rapidly to salt stress of this magnitude. This is consistent with our observation that NDVI at graminoid and dwarf shrub sites dropped to levels below 0.2 the year after the storm. NDVI values  $<0.2$  are typically associated with very low phytomass and percentage cover (Laidler et al. 2008, Raynolds et al. 2012).

It is unlikely that the observed vegetation dieback was caused by submergence during the storm. Climate data from Shingle Point, (60 km to the SW) show that

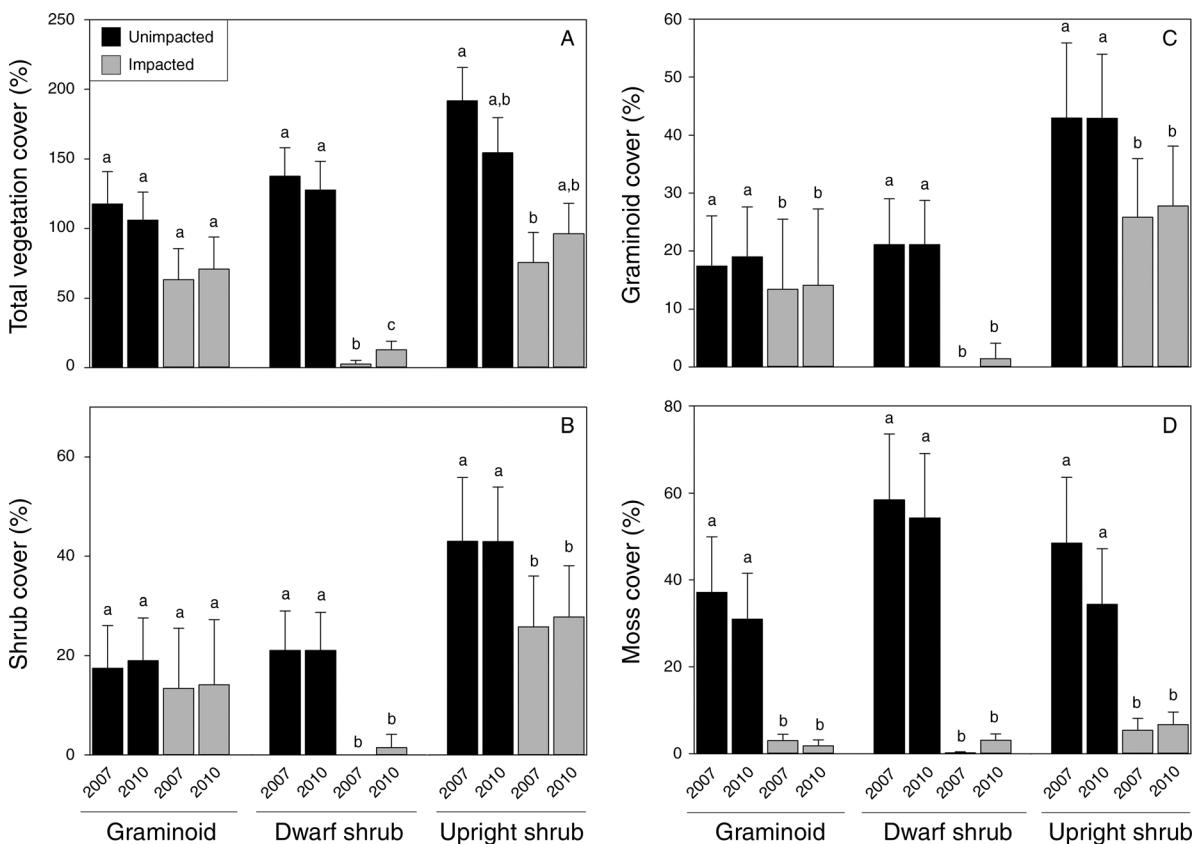


FIG. 4. Vegetation cover by functional group measured in different vegetation types in impacted and unimpacted portions of the outer Mackenzie Delta in 2007 and 2010. Bars show means for: (A) total vegetation, (B) shrub, (C) graminoid, and (D) moss cover. Error bars show the 95% confidence intervals of the mean (untransformed). Within each vegetation type, bars with different letters above them are significantly different ( $P < 0.05$ , mixed-model ANOVA).

temperatures in the outer delta had already declined below  $-2^{\circ}\text{C}$  on four occasions before the storm began on 24 September (Environment Canada 2013). This clearly indicates that the vegetation in the outer delta was already dormant when the storm occurred. This conclusion is also supported by intra-annual NDVI trends across a range of sites in Arctic Alaska (Jia et al. 2004).

Observed differences in recovery among vegetation types were likely driven primarily by the effect of landscape position on the frequency of spring flooding in the years following the storm. Gauge data from Reindeer Channel show that since 1999 there have been 11 events where the river has risen 1 m above the mean, but only one spring flood where the river level exceeded the mean by 2 m (Table 3). Differences in conductivity and chloride levels suggest that more frequent spring flooding in low-lying terrain proximate to channels (graminoid and upright shrub sites) functions to flush salts from these soils. A decline of soil salinity at these sites has likely facilitated observed increases in NDVI and movement toward pre-disturbance plant community composition. This interpretation is also consistent with the coincidence of increases in NDVI and reductions in electrical conductivity below the threshold for saline soils at upright shrub and graminoid sites (Figs. 2 and 6) (2.0 dS/m [Richards 1954]). Conversely, more elevated dwarf shrub sites distant from major channels have experienced less frequent flooding and showed little recovery. Eleven years following the storm, soil pore water electrical conductivities (EC) at these sites still exceeded 4 dS/m, and community composition, productivity, and vegetation structure remained totally dissimilar to unimpacted sites.

Despite the persistent lack of recovery at dwarf shrub sites, it is unlikely that saline inundation has created an alternative stable state, as has been observed in the overgrazed wetlands of the Hudson Bay Lowlands (Jefferies et al. 2006). At these sites, feedbacks initiated by grubbing by geese yield soil chloride levels an order of magnitude higher than the impacted parts of the outer Mackenzie Delta (Srivastava and Jefferies 1995, 1996, McLaren and Jefferies 2004). Revegetation in areas with salinities much higher than measured at our sites (Bazely and Jefferies 1986, Hik et al. 1992) also suggests that recovery is possible at dwarf shrub sites. There is also no evidence that plant communities at our sites are being replaced by salt-tolerant assemblages, as has been observed in other regions (Baldwin and Mendelsohn 1998, Teh et al. 2008, Steyer et al. 2010). This is likely because the most common salt-tolerant species (*Puccinellia phryganodes* (Trin) Scribn. and Merr., *Carex subsppathacea* Wormskj, *Stellaria humifusa* Rottb.) are adapted to moist to hydric soils (Corns 1974, Jefferies 1977, Aiken et al. 2007, Klinkenberg 2013) and the saline soils at dwarf shrub sites are too dry to support their recruitment and survival. Many of these species are also poor dispersers that frequently rely on clonal

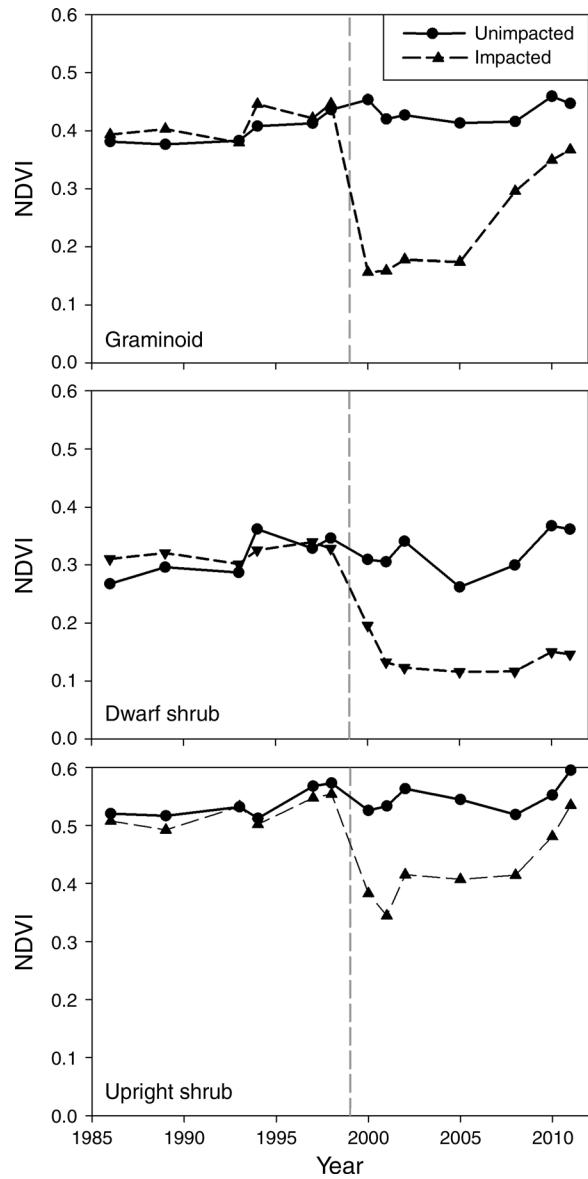


FIG. 5. Normalized Difference Vegetation Index (NDVI) change (1986–2011) in three vegetation types in the outer Mackenzie Delta. Plots show the average top-of-atmosphere NDVI in impacted (triangles connected by a dashed line) and unimpacted (circles connected by a solid line) portions of the study area. The dashed vertical line shows the year of the storm surge.

reproduction (Jefferies et al. 2006). Given the moderate salinity of the soils at dwarf shrub sites, it is likely that continued leaching of soil salts and gradual reductions in conductivity will facilitate recovery in subsequent decades. Ultimately, tracking the successional trajectories at these sites will require ongoing monitoring.

Standish et al. (2014) have recently emphasized the need for research cataloging the ecosystem properties that can be used to predict resilience to future disturbances. Our observations in the outer Mackenzie

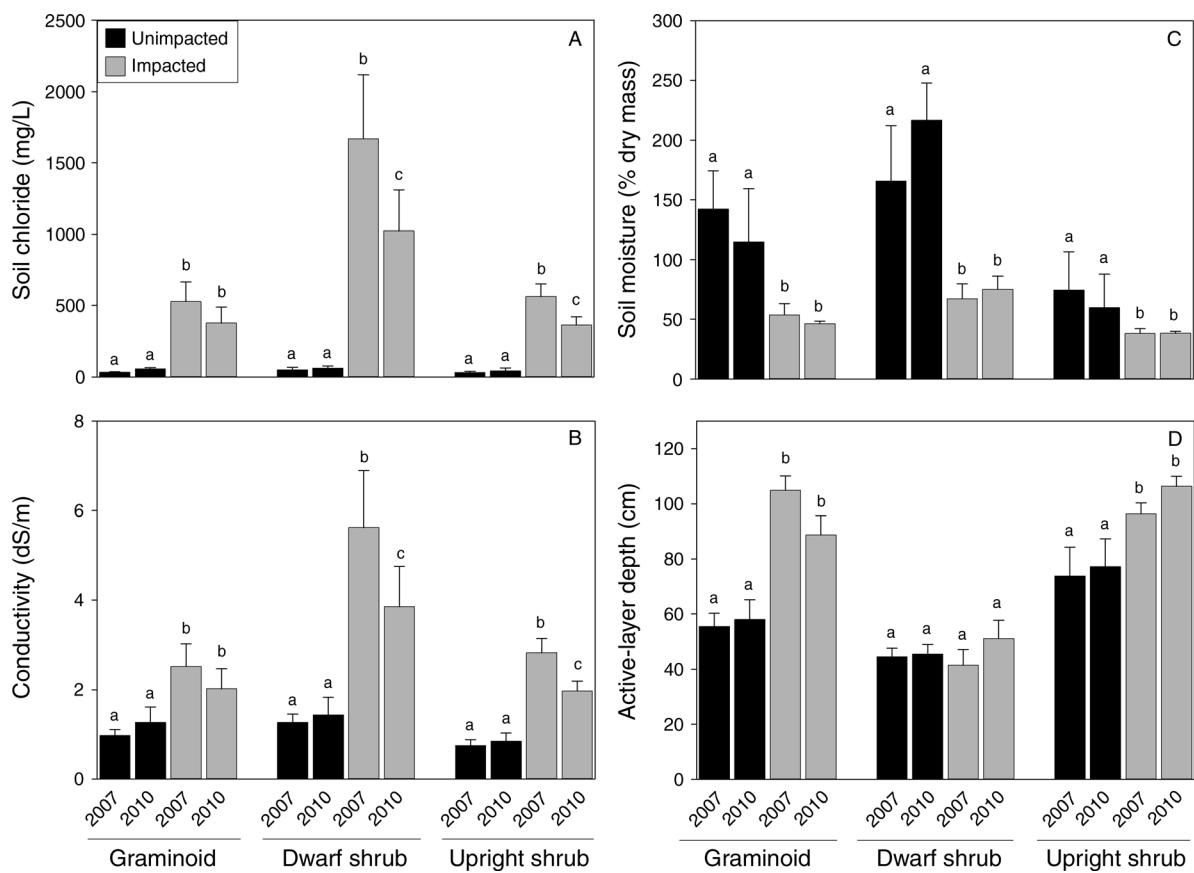


FIG. 6. Soil properties measured in different vegetation types in impacted and unimpacted portions of the outer Mackenzie delta in 2007 and 2010. Bars show means for: (A) conductivity, (B) chloride concentration, (C) moisture, and (D) active-layer depth. Error bars show the 95% confidence intervals of the mean (untransformed). Within each vegetation type bars with different letters are significantly different ( $P < 0.05$ , mixed-model ANOVA).

Delta suggest that the nature of historical disturbance regime may provide an indication of potential resilience to novel forms of disturbance. Our observations show that the plant communities at sites more frequently impacted by freshwater flooding recovered more rapidly following a salinization event, with a magnitude unprecedented in the last millennium. The more rapid recovery of frequently disturbed communities may be linked to higher functional diversity at these sites (Didham et al. 2005, Standish et al. 2014). In the outer delta, recovery was most strongly limited at sites dominated by a suite of species adapted to acidic, nutrient-poor soils (Fig. 3A [Chapin 1987, Gough et al. 2000]). Low functional diversity at these sites likely allows plant communities to tolerate adverse conditions, but limits their ability to recover from other forms of abiotic stress that can follow large disturbances (Ingestad 1973, Simmons et al. 1983, Muralitharan et al. 1992, Eaton et al. 1999, Didham et al. 2005).

The effects of the 1999 storm on community composition and other ecosystem properties have important implications for regional conservation planning. Ecological recovery in the outer delta varied

dramatically by vegetation type. Observations at graminoid and upright shrub sites indicate that functional recovery of these vegetation types to severe saline inundation requires at least a decade. Conversely, a nearly complete lack of recovery at dwarf shrub sites shows that these plant communities likely require several decades to recover from salinization. Combined with the results of plot-scale experiments conducted in Alaska, our data show that areas dominated by dwarf shrubs will be extremely vulnerable to changes in the magnitude and intensity of storm surges, and industrial activities such as water flooding, and sump construction that can result in salt deposition (Simmons et al. 1983, Johnstone and Kokelj 2008).

Areas of dwarf shrub tundra are also the most significant nesting habitat in the outer Mackenzie Delta (J. Rausch, Environment Canada, *personal communication*). With anticipated increases in sea level, storm intensity, and the length of the ice-free season (IPCC 2007, Comiso et al. 2008, Goulding et al. 2009, Knutson et al. 2010), ocean storms causing saline inundation are likely to reduce the quantity and quality of this habitat type. Anecdotal observations from a number of sites

TABLE 3. Number and duration of spring (April, May, and June) flooding events in the outer Mackenzie delta.

Event Magnitude (m)	No. events	No. days	Duration (mean)	Years
0.5	12	222	18.5	2000, 2001, 2002, 2003, 2004, 2005, 2007, 2008, 2009, 2010
1.0	11	136	12	2000, 2001, 2002, 2003, 2004, 2005, 2007, 2008, 2009, 2010
1.5	7	24	3.4	2001, 2002, 2003, 2004, 2005, 2008, 2009
2.0	1	2	2	2005

across the western Arctic suggest that this may already be occurring (Gregory et al. 2006, NSSI 2009, Ecosystem Classification Group 2012, Obst et al. 2013). Such changes highlight the need to account for ongoing habitat loss in ecosystem planning. For example, it was widely expected that proposed gas extraction in the outer Mackenzie Delta region would cause terrain subsidence and alter the availability of nesting and staging habitat in the region. During the Joint Review Panel hearings for the Mackenzie Gas Project, the possibility that other areas of the outer delta should be used to offset these potential impacts was discussed, and the creation and implementation of a habitat offset plan were included as recommendations to the Government of Canada in the final report (Joint Review Panel for the Mackenzie Gas Project 2010). Our work showing that 40% of the low-lying area outside the Kendall Island Bird sanctuary was impacted by the 1999 storm surge makes it clear that the viability of this plan depends on knowledge of current habitat and predictions about future conditions. It also emphasizes the importance of broader spatial planning and cumulative impact assessment that considers the dynamic nature of both natural and human disturbance.

#### CONCLUSIONS

In rapidly changing environments, anticipating the nature of ecological change is a vital component of resilience-based planning. The data presented here show that the impact of saline inundation on tundra ecosystems will depend strongly on vegetation type, with recovery times varying widely. It is anticipated that changes to the earth's climate system will increase the frequency and magnitude of ocean storms, and that Arctic coastal inundation will become more common. As such, significant alterations to ecosystem structure and habitat availability can be anticipated. Our observations indicate that the historic disturbance return interval (freshwater flooding) may provide a good indicator of the resilience of tundra plant communities to saline inundation. It is clear that accounting for storm surge disturbances will be a critical consideration in planning and management activities pertaining to Arctic coastal ecosystems. Research that combines field sampling with regional-scale remote sensing will be vital in the efforts to detect and understand these changes.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–D are available online: <http://dx.doi.org/10.1890/14-0239.1.sm>