Assessing ecological effects of storm surges on Arctic bird populations in the outer Mackenzie Delta, Northwest Territories

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Abstract

Coastal areas in the Western Canadian Arctic are predicted to experience increases in the frequency and intensity of storm surges as rapid climate change continues. Although storm surges have the potential to cause widespread and persistent vegetation loss, little information is available about the influence of decreasing disturbance intervals (between storms), expected timelines of recovery for vegetation, and how vegetation change alters habitat availability and/or quality for local wildlife populations. We investigated how Arctic bird diversity is affected by heterogeneous vegetation recovery post-storm. We employed field survey protocols from the Program for Regional and International Shorebird Monitoring (PRISM) to investigate how avian community assemblage was affected by heterogeneous re-vegetation 20 years following a record 1999 storm surge. Comparisons of this bird survey data with vegetation and habitat factors showed that the drier, post-storm vegetation barrens were preferred by ground-nesters and species that use open habitats such as Lapland longspur (*Calcarius lapponicus*) and semipalmated plover (*Charadrius semipalmatus*), whereas the wetter (usually with surface water) revegetated habitats were frequented by species of ducks (*Anas*spp.), red-necked phalarope (*Phalaropus lobatus*), and savannah sparrow (*Passerculus sandwichensis*). Overall, this research shows that areas that have revegetated after the 1999 storm can be considered as functionally recovered in comparison to our Reference (i.e., unaffected) sites in terms of vegetation and bird communities, but that areas still exist ~20 years post-storm that do not show evidence of recovery.

Keywords

Arctic birds, disturbance regime, climate change, Mackenzie Delta, Arctic vegetation, saline incursion, storm surge.

1 Introduction

Climate-driven habitat alteration poses a significant threat to many bird species (Wauchope, ***et al.***, 2017). Of the ~200 species of birds that are known to breed in the Arctic, 162 are considered to have the majority of their breeding ranges there (Ganter and Gaston, 2013). For this reason, the Arctic Council's Circumpolar Biodiversity Monitoring Program (CBMP) has designated birds as "Focal Ecosystem Components" for monitoring under their terrestrial monitoring program (Christensen, et al., 2013). Of these 162 species with mainly Arctic breeding grounds, 88 are landbirds (Smith, et al., 2020). Fifteen species of shorebirds (out of the 47 total Canadian species) breed exclusively in the Arctic (Donaldson, et al., 2000) and several others include the Arctic within their breeding range. Though they are among the most numerous and species-rich taxa of Arctic waterbirds, many shorebird populations are declining (Jehl, 2007; Morrison, et al., 2013; Clemens, et al., 2016; Piersma, et al., 2016; Wauchope, et al., 2017; Smith, et al., 2023). Additionally, though passerines are ubiquitous and abundant in the tundra, recent trends show declines across taxa in North America during the past decade or more (Rosenberg, et al., 2019; Smith, et al., 2020). Many studies list shifts in habitat characteristics and phenology due to climate change as primary factors in these declines (Baker, et al., 2004; Gaston, et al., 2005; Robinson, et al., 2005; McKinnon, et al., 2012; Senner, et al., 2014; Duijns, et al., 2017; Senner, Stager, and Sandercock, 2017; Studds, et al., 2017). Anthropogenic changes along long migratory routes that can stretch from the Arctic to southern South America may also be contributing (Studds, et al., 2017; Reed, et al., 2018).

Within the next 100 years, climate change is projected to be more rapid and uniform across the Arctic in comparison to historic warming events (Intergovernmental Panel on Climate Change (IPCC), 2013). This suggests the potential for more severe constriction of shorebird breeding distributions than in previous “bottle-necking” events of the mid-Holocene where extreme cold and arid conditions of Quaternary glaciations would have geographically restricted available breeding habitat (Wennerberg, et al., 2002; Buehler and Baker, 2005; Conklin, et al., 2016; Wauchope, et al., 2017). A recent study assessing projected shifts in the spatial distribution of suitable habitat for Arctic-breeding shorebirds predicts considerable northward constriction at a pan-Arctic scale (Wauchope, et al., 2017). These predictions specified the Canadian Arctic Archipelago as being a globally important refuge for shorebirds in the future, but also noted that these habitats currently lack government protection (Wauchope, et al., 2017). Concurrent habitat shifts predicted at breeding sites include the advancement of southern predator ranges (e.g., red fox, *Vulpes vulpes*) and the expansion of potential interspecific competitors (Callaghan, et al., 2004; Killengreen, et al., 2007; Mustin, et al., 2007; Post, et al., 2009), both of which could compound adverse effects already changing shorebird habitat. In addition, some Arctic-breeding shorebird and landbird populations are already suffering from the accelerated advance of spring and increased unseasonal storms as the timing of spring arrival can greatly affect reproductive success and population dynamics (Møller, et al., 2008; Tulp, et al., 2009; Both, et al., 2010; Saino, et al., 2011; Klaassen, et al., 2012; Ganter and Gaston, 2013; Kölzsch, et al., 2015; Smith, et al., 2020). In addition to weather-related issues caused by the advancement of spring, more complex interactions between ecosystems and their inhabitants are becoming apparent as species react to climate and weather pattern changes with various strategies. More evidence with links to specific local effects and drivers is required to tease apart these interactions and predict future patterns in the face of ongoing climate change.

In the circumpolar Arctic, the density and diversity of birds respond to productivity gradients (Smith, et al., 2020). Although heavily vegetated wetlands constitute a small portion of the available habitat, they support a disproportionate richness and abundance of bird species (Smith, et al., 2020). Arctic river deltas are especially critical for migratory birds as stopover, breeding, and nesting grounds (Canadian Wildlife Service, 1992; Latour, et al., 2005), but these low-lying coastal regions are particularly prone to flooding. Although freshwater flooding is a predictable annual event due to upriver snow melt in spring, saltwater flooding events can occur during severe marine weather events (MacKay, 1963; Manson and Solomon, 2007; Vermaire, et al., 2013). Marine storms are expected to increase in frequency and intensity globally as a consequence of climate change (Sepp and Jaagus, 2011). Inuvialuit living in Ulukhaktok, Sachs Harbour, Tuktoyaktuk and other communities in the Beaufort Delta Region have already noted changes in weather patterns that include an increase in strong winds (Berkes and Jolly, 2001; Pearce, et al., 2010; Waugh, et al., 2018). Persistent strong winds in these low elevation areas can produce storm surges, which are defined as an abnormal rise in sea-level along a coastline during a storm (Harris, 1963). These surges can result in the saltwater flooding of riparian and terrestrial ecosystems in a process known as saline incursion, which can cause habitat degradation by killing vegetation that is not salt-tolerant and preventing re-establishment of plant species due to salt buildup in soils (Earle and Kershaw, 1989; Iacobelli and Jefferies, 1991). Previous studies in the Mackenzie Delta (Northwest Territories) show that saline incursion events can be severe enough to cause persistent ecological change (Pisaric, et al., 2011; Vermaire, et al., 2013; Thienpont, et al., 2015). Three previous publications (Pisaric, et al., 2011; Kokelj, et al., 2012; Lantz, et al., 2015) provide evidence that vegetation dieback following the 1999 storm was caused by increased soil salinity. A decade after a storm surge in the delta in 1999, re-establishment of vegetation was underway, but some affected areas remained where little to no recolonization of plants was occurring (Lantz, et al., 2015). However, due to a lack of historical monitoring of similar saline incursion events, approximate timelines for recovery of persistently barren areas remain unclear (Deasley, et al., 2012; Lantz, et al., 2015).

Historically, increased storm surge activity has followed trends of rising temperature and declining sea-ice (Serreze, et al., 2007; Simmonds and Keay, 2009; Vermaire, et al., 2013). The potential for strong winds to produce a surge is also compounded by physical and oceanographic factors such as coastal erosion and sea-level rise (Manson and Solomon, 2007; Nicholls and Cazenave, 2010; Thienpont, et al., 2012). All of these factors are projected to be affected by climate change. With anticipated increases in the potential for saline incursion in Arctic coastal areas, and predicted changes to the distribution of Arctic breeding birds, it will be critical to have a good understanding of potential threats to terrestrial bird habitat in these areas. However, it is currently unknown how vegetation changes from saline incursion in the Arctic are affecting habitat use by bird species and whether affected sites can functionally recover. Since the 1999 storm, several studies have assessed the recovery of soils and vegetation, but to date, no formal investigation of the effects of saline incursion on shorebirds or other avifauna has been conducted (Pisaric, et al., 2011; Thienpont, et al., 2012, 2015; Vermaire, et al., 2013; Lantz, et al., 2015). We used a natural experiment, namely saltwater incursion in portions of the outer Mackenzie Delta, to assess the effects of habitat transformation caused by a severe storm surge on bird community composition and presence. We also conducted field surveys to explore the biophysical factors associated with differences in bird assemblages across the affected area.

2 Materials and methods

2.1 Study Area

The Mackenzie Delta, North America’s largest Arctic delta (~13,000 km^2), is located at the northern continental edge of the Northwest Territories at the outflow of the Mackenzie and Peel rivers into the Beaufort Sea (Burn and Kokelj, 2009; Burn, 2017). The delta is a low-lying alluvial plain with a maximum elevation of ~10 m above sea-level and gradually slopes downward to the Beaufort Sea (Deasley, et al., 2012; Vermaire, et al., 2013). This delta lies within the traditional territory of both the Inuvialuit and Gwich'in peoples, who rely on the land for subsistence (Usher, 2000; Thompson and Millar, 2007). This study focused on the low-lying (< 2 masl; Fig. 1) northern part of the delta (hereafter the "outer delta") (Lantz, et al., 2015). Vegetation in the outer delta can be classified into three dominant vegetation types (graminoid wetland, dwarf shrub, and upright shrub) based on soil characteristics and frequency of flooding (Cordes, et al., 1984; Pearce, 1986; Lantz, et al., 2015). These vegetation types occur in clearly separable bands linked to differences in elevation and distance from distributary channels, with zone boundaries running parallel to distributary channels (Cordes, et al., 1984; Lantz et al., 2015). Vegetation zones in the outer Mackenzie Delta are also much more uniform than tundra to the east and west of the Delta (MacKay, 1963; Cordes, et al., 1984; Pearce, 1986; Burn and Kokelj, 2009). Terrain <30 cm above low tide level is generally unvegetated (Canadian Wildlife Service, 1992).

Within the Mackenzie Delta, the Kendall Island Migratory Bird Sanctuary encompasses approximately 606 km^2 of the outer delta (Canadian Wildlife Service, 1992; Bromley, et al., 2002). Established in 1961, the purpose of this sanctuary was to protect migratory birds (primarily waterbirds) (Canadian Wildlife Service, 1992). Over 100 species of birds have been recorded in the sanctuary, including passerines, shorebirds, and waterfowl (Canadian Wildlife Service, 1992; Environment and Climate Change Canada, 2019). Lesser snow geese (*Anser caerulescens*) use the area as a nesting and staging ground in the fall and constitute a large portion of the waterbird species (Canadian Wildlife Service, 1992). Notable species include Hudsonian godwit and longbilled dowitcher, which have limited breeding grounds in Canada (Canadian Wildlife Service, 1992).

Gravitational tides in the outer delta are small (< 0.5m) in comparison to storm surge events, which can reach around 2.5 m above mean water level (Forbes and Frobel, 1985; Harper, et al., 1988b; Solomon, 2005). Storm surges are a regular occurrence in the outer delta during the open-water months (June-October) but occur more frequently in late summer and into autumn (Solomon, et al., 1994; Atkinson, 2005; Kim, et al., 2021). Not all storm surges result in saline incursion, because freshwater river discharge and wind direction typically keep the saltwater from reaching upstream (Carmack and Macdonald, 2002). However, as river discharge decreases over the open-water season, the potential for storm surges to cause saline flooding inland increases (Yang, et al., 2015; Scharffenberg, et al., 2020). This potential is increasing due to the extended open water, which extends the period when storms can develop and impact the coast (Manson and Solomon, 2007; Overeem, et al., 2011; Vermaire, et al., 2013).

A particularly anomalous surge occurred in 1999 and was retroactively documented (Pisaric, et al., 2011; Kokelj, et al., 2012; Lantz, et al., 2015). Paleolimnological studies have shown that the magnitude of this storm surge was unprecedented in the last millennia (Pisaric, et al., 2011; Vermaire, et al., 2013). Previous studies assessing the ecological consequences post-1999 show that the incursion of saline water was severe enough to cause widespread and persistent (7-10 years post-storm) vegetation kill in ~120 km^2 of the outer delta (Pisaric, et al., 2011; Vermaire, et al., 2013; Thienpont, et al., 2015). A decade after the storm surge in 1999, recovery was occurring slowly, but it was spatially variable with some areas showing no re-establishment of vegetation (Lantz, et al., 2015). Prior to the 1999 storm unvegetated parts of the study area were confined to the edge of distributary channels and the delta front (Kokelj et al., 2012). Though salt-tolerant species are present in the outer delta, previous surveys have not observed them colonizing affected areas, suggesting that this large-scale salinization event was unprecedented in recent history (Pisaric, et al., 2011; Lantz, et al., 2015).

2.2 Site Selection

To explore the impacts of storm-surge driven vegetation change on avian community composition and the abundance of three focal species, we conducted field studies within and outside areas affected by the 1999 surge. Specifically, we sampled areas of the outer Mackenzie Delta in three site types (Revegetated post-salinization, Unvegetated post-salinization (i.e. unrecovered), and unaffected (Reference)).

To delineate the area affected by the 1999 storm surge, we analyzed imagery from the LANDSAT 5, 7 and 8 satellites. Top of Atmosphere (TOA) imagery with less than 20% cloud cover obtained during the peak greening period (July 1 – August 15) was used to calculate the Normalized Difference Vegetation Index (NDVI) annually from 1986-2015. NDVI is calculated using the contrast between near-infrared and red reflectance (Tucker, 1979) and represents a measure of green leaf area and phytomass (Riedel, et al., 2005; Raynolds, et al., 2012). Using Landsat scenes from 1986-1994, we characterized inter-annual variation in NDVI before the 1999 storm and used it to establish a threshold of inter-annual variability that represented a significant departure from normal. This threshold was calculated by creating a raster stack of proportional inter-annual change from 1986-1994, where proportional inter-annual change was defined as: $[\mathrm{NDVI}_{\mathrm{YEAR}} - \mathrm{NDVI}_{\mathrm{PREVIOUSYEAR}}] / \mathrm{NDVI}_{\mathrm{PREVIOUSYEAR}}$. Using this stack, we calculated the average inter-annual pre-storm change on a per-pixel basis. This resulted in a single raster layer where pixels were the average inter-annual change in NDVI across all years. The mean (μ) and standard deviation (σ) of this layer were used to define the range of typical inter-annual variation as: $\mu \pm 2\sigma$, or 0.0355 ± 2*(0.1968). Subsequently, the lower limit of this range was used as a threshold to delineate the extent of the area affected by the 1999 surge as $PNDVI_{2001} - PNDVI_{1998} < -0.358$, and unaffected as $PNDVI_{2001} - PNDVI_{1998} \geq -0.358$. Landsat imagery from 2001 (post-storm) was used because the imagery from 2000 was too late in the growing season to accurately represent the summer peak of vegetation greenness.

We selected re-vegetated and unvegetated sites within the affected portion of the outer delta using two methods that used satellite imagery and aerial photographs captured in 2004 (NWT Centre for Geomatics, 2007). In the first site selection method, high-resolution (effective pixel size =~1m; scale = 1:30000) air photos from 2004 (NWT Centre for Geomatics, 2007) were visually inspected. These air photos clearly show areas of bare ground and areas with green vegetation present. To verify that air photos could be used to classify sites as Revegetated or Unvegetated we extracted a subset of 2004 NDVI values from sites classified as vegetated (n=40) and unvegetated (n=44) using air photos (Table 1). This analysis indicates that affected sites undergoing revegetation had NDVI values greater than 0.25 and typically ranging from 0.303 to 0.713 (Table 1). NDVI values at Unvegetated sites had a maximum of 0.25 and generally ranged from 0.094 to 0.215 (Table 1). Based on these differences, we used 0.25 as a threshold to distinguish vegetated from Unvegetated areas within the affected portion of the outer delta (Table 1).

In the second site selection method, we determined the rate of NDVI change within the affected area using a pixel-based Theil-Sen regression of a Landsat NDVI time series (2001-2012). The significance of Theil-Sen slope estimates (using a Mann-Kendall test) was assessed using a threshold of p = 0.10. Within affected areas, significantly trended pixels with positive slope values were classified as Revegetated and pixels with non-significant or decreasing slopes were classified as Unvegetated. This regression-based classification was compared with the air photo-based classification and field sites were selected in areas where the two classifications agreed. Overall, we selected seven replicates within each of the affected site types and six replicates in the Reference type for a total of 20 sites (Table 2; Figure 1).

2.3 Survey Methods

During summer 2019, we measured bird abundance and diversity in the outer delta during the shorebird breeding season (24 June – 4 July) using the Arctic Program for Regional and International Shorebird Monitoring's (PRISM) rapid survey protocol (Pirie, et al., 2012). Typically, the PRISM protocol for monitoring breeding shorebirds that we used in this study is deployed during an early spring survey window (late May and June) since some early breeders begin southward migration soon after nesting initiation in mid-May (Pirie and Johnston, 2012; Weiser, et al., 2018). However, in the Mackenzie Delta, shorebird nesting initiation is limited by flooding during channel break-up (Pirie, et al., 2012). Additionally, although this protocol was created specifically for surveying breeding shorebirds, we were able to record all avian species present in the plots due to low general abundance. Specifically, two observers (F.N.A.S. and a field assistant) carried out walking transects spaced 25m apart in a 400 by 300m plot, repeating transects until we had covered the entire plot. Bird sightings, qualitative landcover types (i.e. tall shrubs, wet-graminoid, barren), and surface water were recorded on a grid diagram of the plot. Photographs and audio recordings were used to ensure correct species identification. If nests were found incidentally, they were recorded and photographed as well. Following the PRISM protocol, 1 nest/probable nest equates to two mature individuals. All surveys were carried out during rainless, daylight hours to minimize weather effects on detection probability. During our time in the field, we completed 20 bird surveys (6 Reference, 7 Revegetated, 7 Unvegetated). Each bird survey took an average of 2 hours to complete. Vegetation and soil surveys were also completed along 100m transects at each site to assess links between presence of birds and fine-scale habitat characteristics. At 11 points along these transects, nested quadrats (4m^2: tall shrubs and 0.25m^2: ground vegetation) were used to estimate the percent cover of vegetation and to measure soil characteristics (thaw depth, organic soil thickness, etc.). Thaw depth was measured using a graduated metal probe inserted into the ground until the depth of refusal. This method works well in the outer delta because alluvial deposits are deep. Plots were spaced at 10m intervals. Composite active layer samples were collected at 6 points along the transect (0m, 20m, 40m, 60m, 80m, 100m) to measure salinity, pH, and moisture content following the methods outlined by McKeague (1978). All vegetation and soil transects were placed within the bird plots perpendicular to the nearest river channel. These 100 m transects and the larger 300x400 m areas surveyed for birds both occurred within highly homogenous habitat areas.

2.4 Remote Sensing

To assess the influence of landscape variability on the abundance of focal bird species, we used the Landsat and Sentinel archives and the Arctic Digital Elevation Model (DEM) to measure surface wetness and elevation in each of the 300x400m bird plot field sites. Surface wetness was mapped by calculating a Modified Normalized Difference Water Index (MNDWI) on Sentinel satellite imagery (from the beginning of July 2019; 10-m resolution) (Du, et al., 2016). Mean elevation was extracted from the ArcticDEM (2m resolution). Distance to the nearest channel was also measured for each site using an MNDWI water mask derived from the Landsat 8 imagery.

2.5 Statistical Methods

To investigate differences in avian community composition among site types and explore community-habitat associations, we used Non-parametric Multidimensional Scaling (NMDS) ordination in combination with an Analysis of Similarities (ANOSIM). This analysis was completed using a Bray-Curtis dissimilarity matrix calculated from the bird count data of the PRISM surveys (McGarigal, et al., 2000). The relationships between habitat characteristics (see below) and community composition were assessed using the *envfit* function in the *vegan* package (Oksanen, et al., 2015) in R (R Core Team, 2020). We also performed a Similarity Percentage (SIMPER) analysis to identify the species making the largest contributions to avian community structure. Specifically, a SIMPER analysis calculates the contribution of individual species to the total dissimilarity score for each pair of site types. The three focal species identified had the highest percentage contribution to differences observed between the site types. To characterize environmental differences among site types, a Kruskal-Wallis test (rank-based analysis of variance) was performed on a suite of variables including: 1) NDVI, 2) MNDWI, 3) distance to channel, 4) elevation, 5) deciduous shrub cover, 6) vascular plant cover, 7) total vegetation cover, 8) soil moisture, 9) thaw depth, and 10) organic soil thickness. Total % cover was calculated by adding the % cover from the 4m^2 quadrat and both 0.25m^2 quadrats together.

We performed focal species analyses to directly assess correlations between our variables of interest and avian species' occurrences. Our three focal species (savannah sparrow (SAVS; *Passerculus sandwichensis*), Lapland longspur (LALO; *Calcarius lapponicus*), and red-necked phalarope (RNPH; *Phalaropus lobatus*)) were identified by the SIMPER analysis and selected for further analysis due to their higher abundance. Differences in the occurrence of these three focal species were assessed by plotting species' abundances versus site type and performing Pairwise

Fisher's Exact tests to assess relationships between habitat variables and focal species' occurrences. We used this analysis to identify potential variables to focus on in future research or in modelling. Abundance data were transformed from counts into incidences (0/1) and habitat variables were converted into 4 categories using their quartile ranges. Each species was then individually evaluated relative to these binned habitat variables: NDVI, MNDWI, distance to channel, elevation, % cover of deciduous shrubs, % cover of vascular plants, total % cover of vegetation. Total % cover was calculated by adding the % cover from the 4m^2 quadrat and both 0.25m^2 quadrats together.

3 Results

3.1 Avian community composition between site types

The multivariate analysis (Figure 2) indicates that bird community composition at Unvegetated sites was significantly different from those at Revegetated and unaffected Reference sites (Table 3). Unvegetated sites were dominated by Lapland longspur, semipalmated plover, and predatory species (i.e. jaegers and hawks), while Reference and Revegetated sites were dominated by savannah sparrows and red-necked phalaropes (Table 4). Three "focal" species (identified by the SIMPER analysis; savannah sparrow, Lapland longspur, and red-necked phalarope) contributed to 45-61% of the dissimilarity among site types (Table 5; Supplementary Table 1). The variation in avian community composition within site type categories was the lowest in the vegetated sites (Reference and Revegetated) and highest in the Unvegetated sites (Table 4). The multivariate analysis also showed that bird community composition was highly correlated with field and remotely sensed measurements of habitat. Plots dominated by savannah sparrows and red-necked phalaropes were wetter and had higher vegetation cover than plots dominated by Lapland longspur and semipalmated plover; the latter were dry and had low vegetation cover (Figure 2).

3.2 Characterization of environmental differences among site types

As expected, Unvegetated sites had significantly lower vegetation cover and lower NDVI in 2019 compared to Reference and Revegetated sites (Figures 3A, 3B). Unvegetated sites were also drier, showing lower MNDWI (site scale: 120 000m^2) and volumetric moisture content (plot scale: 4m^2) (Figures 3C, 3D), and were located farther from freshwater channels than either Reference or Revegetated sites (Figure 3E). Unvegetated sites had higher mean elevation than Reference sites but the difference was not significant. Unvegetated sites had similar elevation to Revegetated sites. Reference and Revegetated sites also had similar percent vegetation cover, NDVI in 2019, MNDWI, soil moisture, and distance from channel (Figures 3A-E).

Reference sites were all dominated by sedges and variable cover of low shrubs. All Reference sites were consistently wet, and some had standing water. Revegetated sites were typically dominated by wet graminoid habitat, often interspersed with small areas of shrub/herb tundra (MF_1, MF_2 and MD_1). All these sites except one (MF_1) had some amount of standing water. Unvegetated sites were characterized by the dominance of bare ground (Figure 4).

3.3 Focal species assessment

The focal species assessment showed that savannah sparrow and Lapland longspur did not co-occur at any of the sites we sampled (Figure 5). Savannah sparrow were only observed at Reference and Revegetated sites where NDVI was > 0.2 and Lapland longspur were only observed at Unvegetated sites (Figure 5A). Unvegetated sites were > 300m from the nearest channel and had NDVI < 0.25 (Figure 5A-B).

Focal species' occurrences were correlated with vegetation cover and habitat wetness (Table 4). Savannah sparrows were never present at unvegetated sites (Figure 5), and they preferred sites with more vegetation cover (Supplementary Figures 1A, 2C). They also preferred sites that were closer to channels and that had higher moisture (Supplementary Figures 1B, 2D). Lapland longspur were never present at Revegetated or Reference sites (Figure 5) and they preferred sites with low vegetation cover and moisture further from channels (Supplementary Figure 3A-D). Red-necked phalarope were absent from all Unvegetated sites but one and preferred sites with moderate to high cover of vegetation that were an intermediate distance from channels (Supplementary Figures 2C,2D).

4 Discussion

4.1 Main findings

Our analysis indicates that mesoscale differences in bird community composition and the occurrences of focal species were driven by the persistent effects of the 1999 storm surge on habitat. In our study, avian community assemblages were correlated with vegetation structure and productivity as reflected in post-storm NDVI values (Figure 2). Additionally, all of our focal species showed strong associations to NDVI values from Landsat images acquired during the field season (2019) (Supplementary Figures 1-3).

These results are consistent with available information on species' natural histories. Lack of ground cover and surface water at Unvegetated sites clearly made them unsuitable for species that occupy aquatic habitat, such as red-necked phalaropes and ducks, or materials for camouflaging their nests and perching, such as savannah sparrows. Savannah sparrows favour dense ground vegetation, especially grasses, and moist microhabitats since they require material to cover nests and to hide from predators (Wheelwright and Rising, 2020). In contrast, red-necked phalarope breed at or near lakes and pools with marshy margins, where their nests are rarely > 20 m from a source of water (Rubega et al., 2020). Their nests are sometimes concealed in clumps of sedges or grasses or under other low vegetation (Rubega et al., 2020) so they typically prefer pools with emergent vegetation (Rubega et al., 2020).

The strong association between Unvegetated sites and a particular suite of species shows that vegetation die-back following saline incursion could have shifted the relative abundance of birds. Unvegetated sites were characterized by bare ground and the absence of surface water and were dominated by Lapland longspur and semipalmated plover along with various predatory birds (such as jaegers and hawks) that prefer these conditions. In a summer study on Bylot Island (Nunavut), Lapland longspur were observed foraging mainly at margins of dense vegetation or in areas with sparse clumps of plants on margins of barren spots (Hussell and Montgomerie, 2020). Although some prior studies have indicated that Lapland longspur prefer low-canopy vegetated habitats (Boal and Andersen, 2005), we observed them (both audio and visual observations) only in Unvegetated sites.

Though not particularly abundant in our study, semipalmated plover also showed clear preference for the Unvegetated sites. This is likely because they require open, flat ground for running and foraging (Smith and Nol, 2000; Nol and Blanken, 2020). In habitat selection studies on Akimiski Island (Nunavut), semipalmated plover showed preference for open, pebbled areas and muddy habitats for breeding and nesting (Nguyen et al., 2003; Nguyen, et al., 2013). Additionally, many species observed in Unvegetated sites were predatory (parasitic jaeger, rough-legged hawk, and a short-eared owl (*Asio flammeus*)). It is possible that these species prefer hunting in these habitats where there is no cover for prey (Liebezeit, et al., 2009). We did observe territorial behaviours (alarm calling and circling) by the jaegers and hawks, so it is possible that some of these species are also using these habitats for breeding.

Our analysis suggests that revegetation 20 years following the storm surge has been adequate to restore habitat functionality for certain avian species at some sites. Avian community composition, focal species' identities, and habitat conditions were functionally similar between unaffected Reference and affected Revegetated sites. Prior to this study, we were unsure whether birds would avoid returning to affected but revegetated areas. We also had no reference for the threshold at which enough vegetation reestablishment would overcome potential avoidance behaviour. Observations made in this study indicate that these Revegetated sites have sufficient vegetation cover to host similar avian populations as the unaffected Reference sites, however, more targeted studies of bird species' habitat selection along gradients of vegetation, soil moisture, and surface water are still required.

From a strictly observational standpoint, the structure of the vegetation communities between the two vegetated site types appeared different on the ground. Reference sites had more shrub cover overall and/or more tall shrubs, whereas Revegetated sites tended to be mostly covered in sedges, some quite homogenously so. Despite these observed differences in plant community composition between the vegetated site types, the avian communities at these sites were similar, suggesting that functional recovery occurs within twenty years of vegetation loss in a productive Arctic delta, at least from the perspective of breeding birds. Further analysis of the vegetation cover revealed no significant differences between Revegetated and Reference site communities in terms of plant species assemblages (Shipman, 2023). The avian species present at Revegetated sites were more consistent, with assemblages between sites being different due to changes in avian species richness rather than identity. This could be attributed to the relative homogeneity of the vegetation community and habitat structure at the Revegetated sites (Brandolin, et al., 2016; Smith, et al., 2020). Vegetation community composition aside, both vegetated site types were quite wet, consistently having standing water available. Although we found low differences (Table 3) in avian community composition between Revegetated and Reference sites, we found nests and/or nesting behaviours by ducks, Wilson's snipe (*Gallinago delicata*), and red-necked phalarope only at Revegetated sites. In total, 6 nests from different bird species were found in 5 separate sites, however no evidence of nesting (or "probable nesting") was found in Reference sites. This could point towards some species using these two habitat types for different purposes, but further study over a longer period is required to confirm these patterns.

4.2 Significance

Our study shows that the persistent impacts of terrestrial salinization following the 1999 storm have altered avian community composition in affected areas of the delta. Remote sensing estimates from 2019 suggest that ~3345 ha (~13% of the originally affected terrestrial surface area) have not recovered (to threshold 0.25 NDVI). To our knowledge, this is the first systematic study assessing the effects of terrestrial habitat change from saline incursion on Arctic birds. Our analysis suggests that habitat changes from more frequent and severe storm surges could alter bird community composition and perhaps the abundance of individual species. Vegetation loss creates habitat conditions that are avoided by certain species but selected for by others. With climate change resulting in recurrent and severe changes to future seasonal temperatures and sea-ice condition, extreme weather events in the Mackenzie Delta such as storm surges are likely to become the norm rather than the exception (Atkinson, 2005; Simmonds and Keay, 2009; Sepp and Jaagus, 2011). With this projected increase in storm surge frequency and intensity, the potential for additional areas to become persistently unvegetated also increases, something that highlights the importance of considering the cumulative effects of repeated storm surges and disturbances associated with permafrost thaw, increasing oil and gas development, and other anthropogenic disturbances (Barry and Spencer, 1976). Our results provide insight into how future vegetation changes may affect habitat availability for some avian species, contributing to improved predictions of how climate changes will affect Arctic bird populations in the Mackenzie Delta and beyond. Although extrapolation of conclusions from this study is limited by our single season of data collection, ongoing monitoring of bird populations and vegetation change in the outer Mackenzie Delta is vital to assess the effects of inter-annual variation, to determine drivers of habitat recovery and thresholds of habitat selection for birds, and to assess the relative effects confounding variables that we could not isolate in our study. We believe that the information from this and future studies is critical to effective impact assessments and protected area management for Arctic breeding birds in the face of ongoing development decisions.

4.3 Conclusion

This natural experiment of saltwater incursion in portions of the outer Mackenzie Delta provides evidence that vegetation changes in storm-surge-affected habitats can have significant and lasting effects on habitat suitability for avian species. The degree to which each individual species will be affected by this habitat loss or degradation will depend on the compounding effects of several factors, including those presented in this study and pressures from outside their breeding territory. Since breeding success drives population size and diversity, the maintenance of Arctic-breeding bird populations depends on the ability of each species to use patchily distributed habitat in a changing Arctic landscape. Currently, there is limited information available on the breeding success of Arctic bird species in the face of breeding habitat shifts and reduction. This study has provided novel, valuable baseline data for the use of habitat damaged by saltwater intrusion by birds in the Mackenzie Delta. Understanding the impacts of large-scale salinization events on habitat availability for breeding birds is important for current and future monitoring and conservation efforts, especially for avian species that breed exclusively in the Arctic.

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Author contribution statement

Study Design: FNAS and TCL, Fieldwork and Analysis: FNAS and TCL, Writing: FNAS, Revisions and Editing: FNAS, TCL, and LKB.

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Data availability statement

The metadata for this analysis will be uploaded to the Polar Data Catalogue and data are available by request from the authors.

Competing interests statement

The authors declare there are no competing interests.

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Tables and Figures

Table 1. Summary of vegetated versus unvegetated NDVI values in 2004.

Unvegetated			**Vegetated**		
Mean	Mean + 2*SD	Maximum	Mean	Minimum	Mean – 2*SD
0.1347	0.2154	0.2507	0.5080	0.2500	0.3033

Table 2. Summary of site selection criteria using NDVI from Landsat imagery.

Site type	Classification criteria
Unaffected / Reference (n=6)	– $PNDVI_{2001}$- $PNDVI_{1998}$ > -0.358
Affected / Revegetated (n=7)	– $PNDVI_{2001}$- $PNDVI_{1998}$ < -0.358 – Significant increasing trend in NDVI from 2001-2012 – Green vegetation visible on 2004 air photos. – $NDVI_{2018}$ > 0.25
Affected / Unvegetated (n=7)	– $PNDVI_{2001}$- $PNDVI_{1998}$ < -0.358 – No trend in NDVI from 2001-2012 – No green vegetation (brown) visible on 2004 air photos. – $NDVI_{2018}$ < 0.25

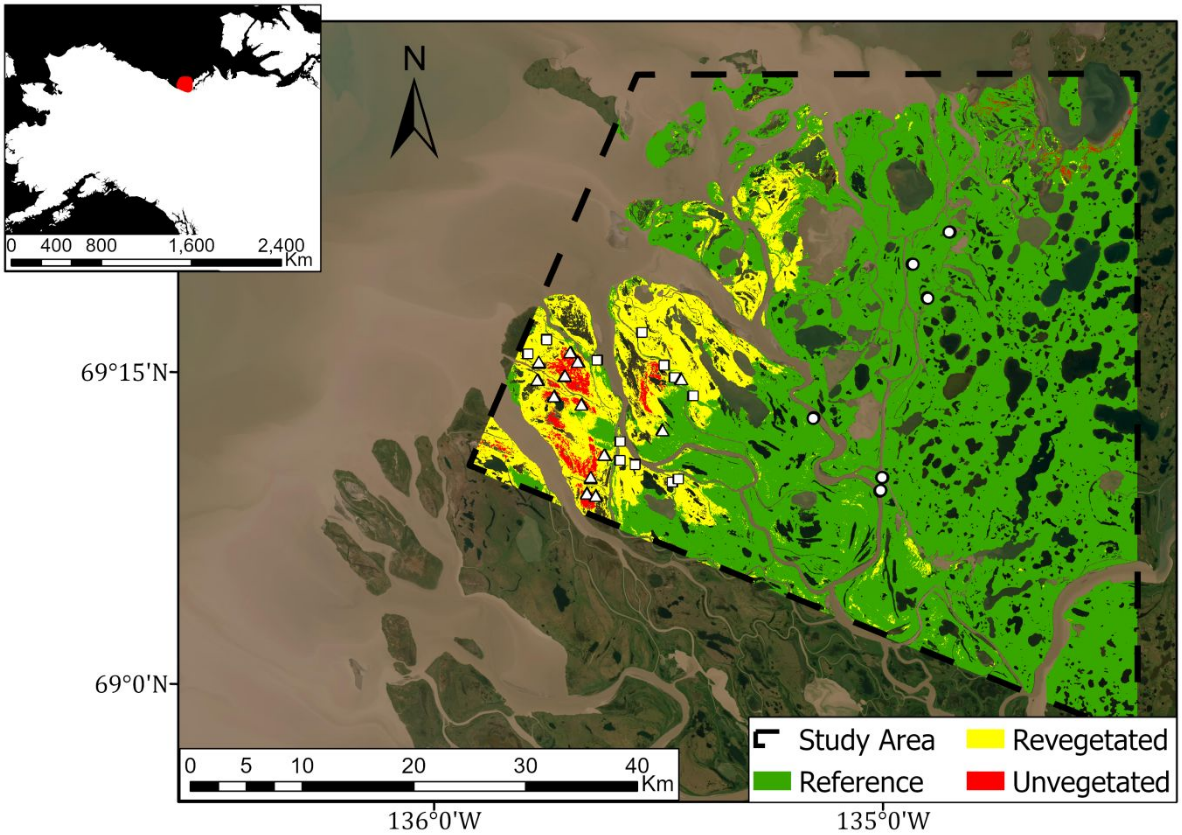

Figure 1. Map showing the locations of site types sampled in this study: Reference Sites (●), Revegetated Sites (■), and Unvegetated Sites (▲). Sites were selected using the classification criteria in shown in Table 2.

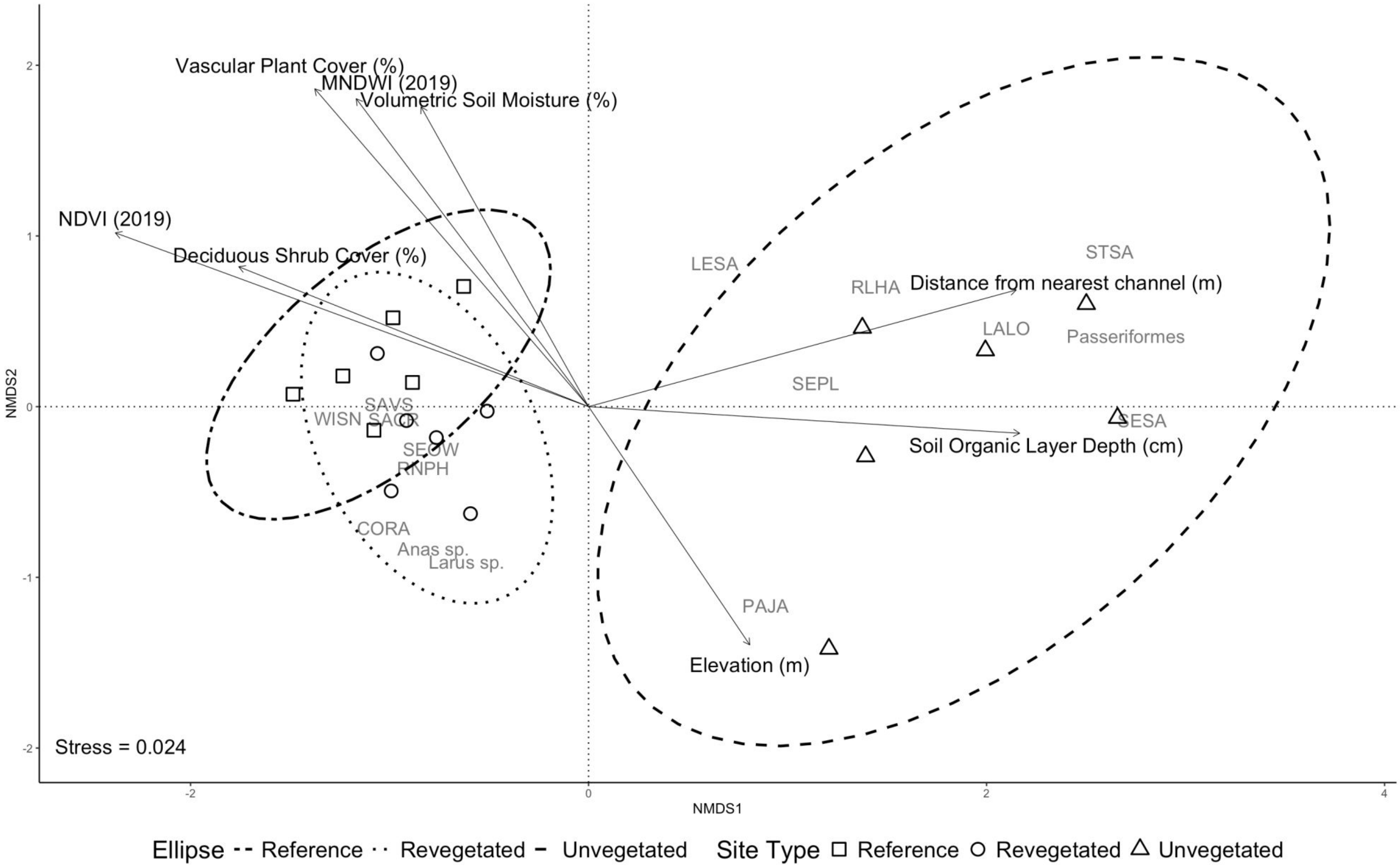
Vascular Plant Cover (%)
MNDWI (2019)
Volumetric Soil Moisture (%)
NDVI (2019)
Deciduous Shrub Cover (%)
LESA
STSA
RLHA
Distance from nearest channel (m)
LALO
Passeriformes
SEPL
SAVS
WISN
SACR
SESA
SEOW
RNPH
Soil Organic Layer Depth (cm)
CORA
Anas sp.
Larus sp.
PAJA
Elevation (m)
Stress = 0.024
NMDS2
NMDS1
2
1
0
-1
-2
-2
0
2
4
Ellipse
Reference
Revegetated
Unvegetated
Site Type
Reference
Revegetated
Unvegetated

Figure 2. Non-parametric multidimensional scaling (NMDS) ordination of bird community composition based on Bray-Curtis similarity. The ordination shows the NMDS scores for each site type (open shapes) and correlations between biotic and abiotic habitat variables and NMDS scores (solid arrows). The ellipses show the 95% confidence zone of each site type assuming a multivariate t-distribution (Wickham, 2016). Bird species are plotted in the ordination according to NMDS scores (calculated using the scores() function from the vegan package in R (Oksanen et al., 2015)). Scientific and common names corresponding to each species' abbreviation are provided in the appendix (Supplementary Table 2).

Table 3. Results of the ANOSIM analysis comparing community composition among site types. The Global R-statistic for this test was 0.589 ($p < 0.001$).

Site types (pairwise combinations)	R_{ANOSIM} statistic	p
Reference / Unvegetated	0.851	0.002
Reference / Revegetated	0.259	0.027
Unvegetated / Revegetated	0.843	0.002

Table 4. Global significance statistics for Fisher's Exact comparing the incidence of focal species with habitat variables. Significant associations are shown in bold text.

Species	Habitat Variable	Global p-value
Savannah sparrow	NDVI in 2019	**0.0047**
	Total cover of vegetation (%)	**0.00068**
	MNDWI in 2019	0.091
	Distance from nearest channel (m)	**0.0047**
Lapland longspur	NDVI in 2019	**0.0088**
	Total cover of vegetation (%)	**0.013**
	MNDWI in 2019	0.38
	Distance from nearest channel (m)	**0.039**
Red-necked phalarope	NDVI in 2019	**0.0053**
	Total cover of vegetation (%)	0.17
	MNDWI in 2019	1
	Distance from nearest channel (m)	0.24

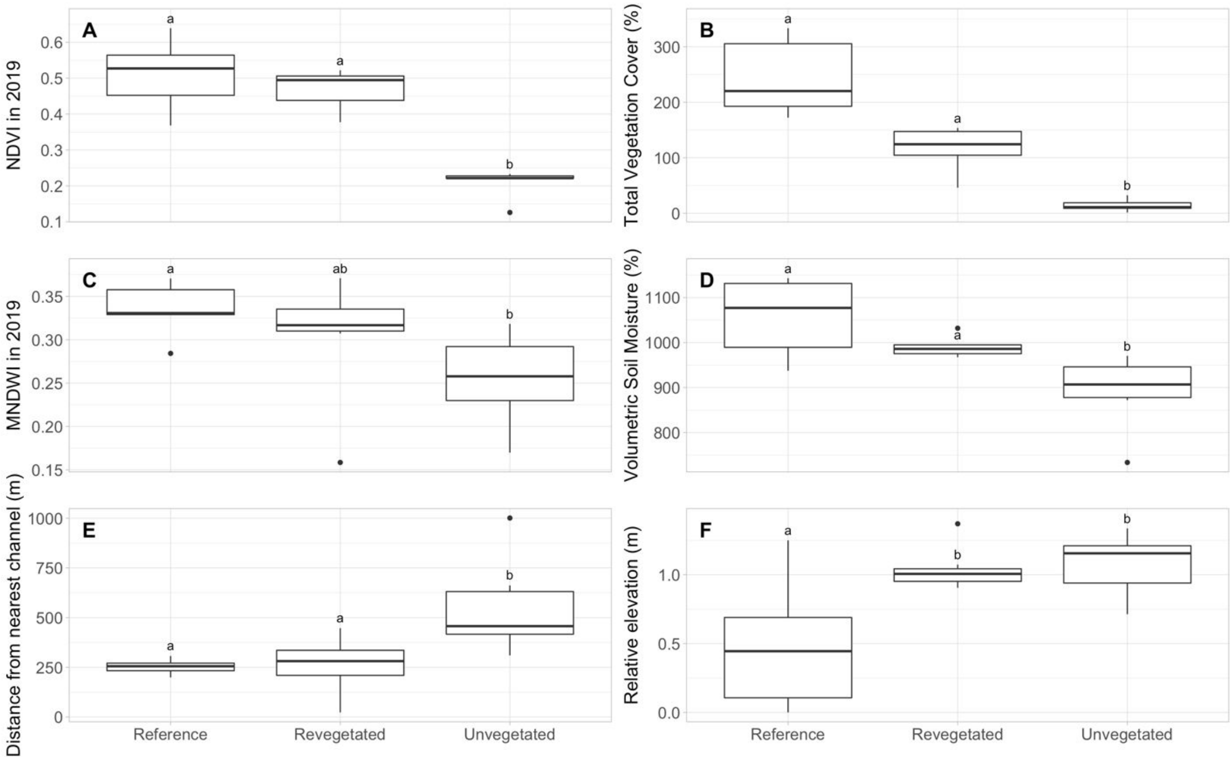

Figure 3. Box and whisker plots showing: (A) NDVI in 2019, (B) Total % cover of vegetation (cumulative % cover from all quadrats: $4m^2$, (a) $0.25m^2$, (b) $0.25m^2$), (C) MNDWI, (D) Volumetric soil moisture (%), (E) Distance from the nearest channel, and (F) Elevation at affected (Revegetated and Unvegetated) and unaffected (Reference) sites in the outer Mackenzie Delta. The horizontal line inside each box shows the median for each site type. The box edges show the 25th and 75th percentiles and the whiskers show [1.5*IQR]. Bars with different letters above them are significantly different ($p \leq 0.05$).

Figure 4. Photos from our 2019 field season of 3 site types. From left to right: Reference (unaffected), Revegetated (affected), Unvegetated (affected).

Figure 5. Gradient diagrams showing the number of savannah sparrows (green) and Lapland longspurs (brown) at sites across the study area. Lapland longspurs were never observed at Reference and Revegetated site types and savannah sparrows were never observed at Unvegetated site types. The grey line on panel (A) shows NDVI in 2019 at each site and the grey line on panel (B) shows the distance to the nearest channel (in meters) at each site. Sites are arranged along the x-axis into their site types.

Table 5. Results of the SIMPER analysis characterizing dissimilarity in bird community composition among three site types. The third column shows the species explaining the majority (>50%) of the cumulative dissimilarity among pairwise site type combinations. Mean abundance of birds per plot (untransformed) of each species at the site types being compared is shown in the fifth column.

Site type combinations	Average dissimilarity (%)	Species	Contribution to dissimilarity (%)	Average abundance at each site type

Reference / Unvegetated	99.00	Savannah sparrow	34.40	2.80 / 0
		Lapland longspur	20.93	0 / 1.83
		Semipalmated plover	7.35	0 / 0.76
Reference / Revegetated	44.05	Red-necked phalarope	31.21	0.35 / 1.74
		Dabbling ducks *(Anas* spp.*)*	15.40	0 / 0.94
		Savannah sparrow	13.77	2.80 / 2.70
Unvegetated/ Revegetated	95.94	Savannah sparrow	27.32	0 / 2.70
		Lapland longspur	17.28	1.83 / 0
		Red-necked phalarope	15.11	0.31 / 1.74

Notes: The top three species making the greatest contribution to the between-group Bray-Curtis dissimilarity for each site combination are shown.