

ARTICLE

Ornithogenic alteration of a tundra ecosystem from decades of intense herbivory and dense nesting

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Handling Editor: C. Jason Williams**Abstract**

Migratory animals can serve as ecological links between geographically distant ecosystems. Moreover, when seasonally linked ecosystems differ in carrying capacity of migrant species, those with high capacity may support population growth with consequences to shared ecosystems with lower capacity through trophic cascades. Agricultural production has increased carrying capacity of lesser snow (*Anser caerulescens caerulescens*) and Ross's geese (*Anser rossii*, collectively, "light geese") in southern agricultural landscapes where these species winter and stage during migration to and from northern breeding areas, resulting in population increase. In subarctic and arctic ecosystems where carrying capacity for geese is lower, high abundance and densities of light geese have caused trophic cascades during summer breeding. This has raised concern for resilience of northern ecosystems to withstand cumulative and intense pressures of above- and belowground herbivory and nest construction. We investigated the empirical relationship between intensity of vegetation disturbance by multidecadal foraging and nest construction by up to ~1.3 million geese and shifts in (1) plant community composition and (2) taxon richness of freshwater plant communities near Karrak Lake, in Canada's central arctic. Intense use by nesting light geese caused shifts from lowland communities dominated by grasses and sedges (collectively, graminoids), *Sphagnum* spp., and willows (*Salix* spp.) to those comprised of exposed peat, non-*Sphagnum* mosses, marsh ragwort (*Tephrosieris palustris*), mare's tail (*Hippuris vulgaris*), and particularly birch (*Betula glandulosa*). Community change was less apparent in upland regions that were naturally less vegetated even in the absence of avian herbivores, but fruticose lichens, crowberry (*Empetrum nigrum*), and white heather (*Cassiope tetragona*) dominated undisturbed plant communities, whereas crustose lichens and bearberry (*Arctostaphylos* spp.) comprised disturbed communities. We did not find evidence for dominance by a limited number of species with long-term occupancy by light geese, as taxon richness was equivocal between disturbed and undisturbed plant communities. Cessation of foraging and nesting pressure increased taxon richness and reestablishment of locally eradicated plant species. Overall, herbivory and

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nesting effects were not uniform across this widespread nesting colony and, together with underlying influence from abiotic gradients, increased heterogeneity in the mosaic of vegetation communities.

KEYWORDS

arctic, birch, graminoids, herbivory, hyperabundant, lesser snow goose, nesting, plant community, Ross's goose, spatial heterogeneity, vegetation

INTRODUCTION

Many grassland ecosystems evolved in response to fire and herbivory, with convergent adaptations to these disturbances as well as to low water availability; typical of plants constituting grassland communities are those with basal meristems, small stature, high densities of shoots, and ample belowground nutrient reserves (Díaz et al., 2007; Huntly, 1991; Nerlekar & Veldman, 2020). Subarctic and arctic ecosystems dominated by grasses and sedges (collectively, graminoids), only rarely subjected to fire (e.g., Jones et al., 2009, but see Beamish et al., 2020), also can be shaped by herbivory (Cargill & Jefferies, 1984; Hik & Jefferies, 1990; Person et al., 1998; van der Wal, 2006), with communities of plant species sharing many of the same traits as those of temperate and tropical grasslands. Northern grazing lawns, created and maintained under optimal levels of herbivory, maintain a steady state of high nutrient content and consist of plant species adapted to grazing by exhibiting prostrate and rapid growth and positive response to nutrient inputs from fecal and urine deposits by herbivores (Cargill & Jefferies, 1984; Hik & Jefferies, 1990; Person et al., 1998; van der Wal, 2006). Despite short growing seasons with limited soil nutrient availability (Porsild, 1964; Shaver & Chapin, 1995), grazing lawns in northern regions demonstrate remarkable resilience to high levels of grazing by regenerating from belowground biomass, often after extensive and virtually complete removal of annual aboveground production (Cargill & Jefferies, 1984; Gauthier et al., 1995; Madsen et al., 2011; Person et al., 1998).

On their northern staging and breeding areas, intense disturbance to vegetation by currently high populations of lesser snow (*Anser caerulescens*) and Ross's geese (*Anser rossii*, collectively, light geese) (Fox & Leafloor, 2018) has had significant consequences for grazing lawns through foraging activities on above- and belowground plant biomass (Abraham et al., 2020; Conkin & Alisauskas, 2017; Fontaine & Mallory, 2011; Jefferies et al., 2006). As well, light geese exhibit fidelity to nesting colony locations (Alisauskas et al., 2022; Wilson et al., 2016) where dense nesting and uprooting of vegetation for nest construction

(Abraham et al., 2020; Alisauskas et al., 2006; McCracken et al., 1997) can lead to revegetation (Abraham et al., 2020; Alisauskas et al., 2006; Samelius & Alisauskas, 2009). Combined and cumulative decadal effects of foraging on above- and belowground biomass and removal of vegetation by nesting activities has resulted in changes to plant communities over a landscape scale. In subarctic coastal regions along western Hudson Bay, exposure of marine sediments following removal of vegetation by geese resulted in changes to plant community species composition (Abraham et al., 2005; Jefferies & Rockwell, 2002; McLaren & Jefferies, 2004; Srivastava & Jefferies, 1996). In these coastal and near-coastal communities, intense foraging of graminoid-dominated communities exposed underlying marine sediments, and increased evaporation from sediments concentrated marine salts and resulted in soil hypersalinity. In turn, hypersalinity impeded graminoid regeneration and produced an alternative stable state of bare sediment that was often colonized by halophytic species (references given above).

Compared with subarctic regions, fewer details are known about changes in community composition of arctic plant communities in response to disturbance by high population abundance and densities of light geese. Remote-sensing investigations (Conkin & Alisauskas, 2017; Didiuk & Ferguson, 2005; Fontaine & Mallory, 2011) have reported dramatic increases in exposed peat following increased abundance of geese. Ground-based investigations have also reported net loss of plant biomass, changes in cover of individual plant taxa and increases in exposed peat and bare mineral substrate, and encroachment of colonizing species (Abraham et al., 2020; Alisauskas et al., 2006; Fontaine & Mallory, 2011; Gauthier et al., 1995; Kellett & Alisauskas, 2022; Samelius & Alisauskas, 2009). However, there have been few multispecies assessments (e.g., Abraham et al., 2020) of arctic plant community response to disturbance by light geese across a range of edaphic states (e.g., upland vs. lowland habitats) and variation in cumulative intensity of disturbance over multiple decades.

At a large nesting colony of light geese in a freshwater arctic ecosystem, we investigated the empirical relationship between intensity and duration of vegetation

disturbance by geese (foraging and nesting) and shifts in community composition of plant communities. We predicted that shifts in community composition to altered communities would be most prevalent in longest-occupied regions of the colony subjected to high nesting densities, and that reduction in taxon richness (an index of species richness, see [Methods](#)) of vegetation may occur in such areas. In response to decades-long and intense nesting by light geese, earlier investigations had identified altered states dominated by exposed peat and exposed mineral substrate (Abraham et al., 2020; Alisauskas et al., 2006; Conkin & Alisauskas, 2017; Fontaine & Mallory, 2011). Our objective in this study was to characterize community composition of these altered states, as well as quantify shifts between vegetation communities in response to intensive use by geese. In hydric and mesic lowland habitats, we predicted that species such as marsh cinquefoil (*Potentilla palustris*) and marsh ragwort (*Tephrosia palustris*) would become prevalent on exposed peat, as occurs in subarctic regions (Kerbes et al., 1990). In xeric upland habitats, we had no predictions about which species may persist or colonize bare substrate, although those resistant to uprooting should be most likely to persist. Further, we monitored response of altered plant communities to cessation of nesting by light geese after continual, multiyear use. We predicted that if sufficient belowground biomass remained in altered communities, as demonstrated by Kellett and Alisauskas (2022), then altered communities could revert to former communities when grazing pressure and nesting density subsides.

METHODS

Study area

The Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary (hereafter, the Sanctuary) is located on the Arctic Coastal Plain of the mainland of Nunavut, Canada. The region is a generally flat plain of postglacial emergence, stretching 300 km along the south coast of Queen Maud Gulf and extending 135 km inland, covering over 62,900 km² of contiguous terrestrial (56,375 km²) and marine (6553 km²) habitat (Environment and Climate Change Canada, 2020). Terrestrial habitat in the Sanctuary ranges from sea level to about 600 m above sea level (asl) and broadly consists of (1) well-vegetated hydric wetland complexes and mesic tundra dominated by sedges, grasses, mosses, and dwarf shrubs (<40 cm in height); (2) streams and shallow lakes; and (3) exposed rock outcrops and boulder and gravel fields sparsely vegetated by lichens and vascular plants (Didiuk & Ferguson, 2005; Environment and Climate

Change Canada, 2020; Walker et al., 2005). Light geese nest in spatially discrete colonies at densities much higher than is typical at other arctic breeding regions (Kerbes et al., 2014). One of the largest known colonies is located at Karrak Lake (Kerbes et al., 2014), about 60 km inland from the coast of Queen Maud Gulf. At the time of its discovery in the mid-1960s, about 17,000 light geese nested on a third of the islands of Karrak Lake (Ryder, 1969). By the onset of intensive nesting studies there in 1991, the nesting colony had expanded to mainland regions surrounding the lake and reached maximum spatial extent in 2011, then occupying over 270 km² of terrestrial habitat, and maximum abundance in 2012, at nearly 1.3 million individuals (Alisauskas et al., 2012; R. Alisauskas, unpublished data).

Field methods

We conducted vegetation surveys timed to correspond to growth phases for all plant species on sample plots within and near the light goose nesting colony at Karrak Lake in mid-July in 1998, 2014, and 2017. We determined locations of systematically spaced plots using the Universal Transverse Mercator (UTM) grid system: the primary purpose of these circular sample plots on which we also conducted vegetation surveys in 1998, 2014, and 2017 was for ongoing annual estimation of nest density, species composition of geese, nest initiation date, clutch size, and nest success of light geese beginning in 1991 (Alisauskas et al., 2012). These plots were spaced at 0.5- or 1.0-km intervals and were of radius 20 m (1991–1995) or 30 m (1996–2017). We determined the spatial extent of the sampling frame for goose nests each year by mapping the colony boundary from a helicopter (Alisauskas et al., 2012). For vegetation surveys, we added plots to the sample region to include locations outside the colony boundary. Due to recent retraction of the colony perimeter, some of these plots outside the colony in 2017 had been inside in the past, while others had never been exposed to nesting by colonial geese, based on historical data (Kerbes et al., 2014).

At each sample plot, we conducted point-intersect surveys described by Alisauskas et al. (2006). We recorded substrate or plant or lichen species or species groups at 0.5- or 1.0-m intervals along 30-m transects extending from the plot center. In 1998 and 2014, we recorded observations in the four cardinal directions (at 1.0-m intervals, resulting in 120 observations per plot). In 2017, due to time restraints, we recorded observations only north of the plot center (at 0.5-m intervals, resulting in 60 observations per plot). We did not identify grasses, sedges, willows (*Salix* spp.), lichens, and mosses to

species, most often because of identification difficulties due to grazing effects or observer inexperience, and instead refer to these categories as species groups (Table 1). In 2017, we discerned lichen species by growth form (crustose, fruticose, foliose, or cup). Plant nomenclature follows Aiken et al. (2007).

Statistical analyses

We performed statistical analyses using the R Statistical Computing Environment (R Development Core Team, 2018) and Program MARK (White & Burnham, 1999).

Multivariate characterization of vegetation communities

We used nonmetric multidimensional scaling (NMDS) with Bray–Curtis distance (package *vegan*, Oksanen et al., 2019) to characterize vegetation communities on sample plots within and adjacent to (i.e., <5 km) the nesting colony of light geese at Karrak Lake in 2017. NMDS is an unconstrained multivariate ordination

technique based on ranked distances which improves ability to extract information from nonlinear relationships between species occurrences (McCune & Grace, 2002; Oksanen, 2015) and is thus often used to explore patterns in community ecology (e.g., Elliott & Vose, 2016). A metric of goodness-of-fit, stress (low stress indicates improved fit), is a function of observed dissimilarities in original data and resulting ordination distances (Oksanen, 2015). We compiled input data by summing point-intersect observations of each species or species group per plot and included only those species and species groups in which occurrence across all plots was greater than 1% to reduce the influence of rare species (Elliott & Vose, 2016; Rettie et al., 1997) but retained those species with known or suspected correlation with high nesting density and intense foraging by colonial geese (Alisauskas et al., 2006; Kerbes et al., 1990). We first constructed ordinations with 1–9 axes, with a maximum of 1000 iterations for each number of axes to determine if convergence was achievable. We determined the appropriate number of axes for the final configuration by seeking low stress values (for ecological community data, stress of <0.20 is acceptable, McCune & Grace, 2002). We then constructed multiple (>10) ordinations with the

TABLE 1 Percent occurrence (number of observations expressed as a percent of the total, in percentage) of species and species groups and resulting axis loadings from a three-axis nonmetric multidimensional scaling (NMDS) ordination of vegetation community data collected on 30-m radius sample plots inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, during 2017 ($n = 256$ plots).

Code	Species or species group	Percentage	NMDS1	NMDS2	NMDS3
LIFRUT	Lichen species, fruticose form	15.7	−0.6899	−0.4326	0.2705
MOOT	Moss species, not <i>Sphagnum</i> spp.	15.0	0.5338	0.0537	0.2217
BIRC	Birch (<i>Betula glandulosa</i>)	14.3	0.4246	0.5751	−0.4504
CRAN	Cranberry (<i>Vaccinium vitis-idaea</i>)	11.4	−0.2491	0.3482	0.0863
LABT	Labrador tea (<i>Ledum palustre</i>)	11.0	−0.4436	0.0856	−0.0883
PEAT	Dead moss species	8.2	0.4729	0.2131	0.2114
GRAM	Graminoids (grass and sedge spp.)	8.1	0.9403	−0.7632	−0.5035
HEAT	Arctic heather (<i>Cassiope tetragona</i>)	3.4	−0.5432	−0.2405	−0.4718
WILL	Willows (<i>Salix</i> spp.)	3.3	0.9508	−0.4419	−0.3474
LICRUST	Lichen species, crustose form	2.7	−0.2785	0.1204	0.3498
SPHA	<i>Sphagnum</i> spp.	1.8	0.9624	−0.6977	0.1871
BEAR	Bearberry (<i>Arctous</i> spp.)	0.9	−0.6924	0.9169	0.4338
CROW	Crowberry (<i>Empetrum nigrum</i>)	0.7	−0.8331	0.1247	0.0151
BLUE	Blueberry (<i>Vaccinium uliginosum</i>)	0.7	0.2765	−0.1918	−0.8147
RAGW	Marsh ragwort (<i>Tephrosieris palustris</i>)	0.5	1.1096	0.3745	0.8455
MACI	Marsh cinquefoil (<i>Comarum palustre</i>)	0.4	1.4850	−0.4497	0.7432
MATA	Mare's tail (<i>Hippuris vulgaris</i>)	0.3	0.7734	0.3653	1.2165

Note: Seventeen species and species groups, each with either >1% representation on sample plots or thought to be indicative of plant community change resulting from foraging and nesting by geese, accounted for 98.4% of point-intersect observations.

chosen number of axes and visually examined the ordinations to ensure reproducibility and stability of the final configuration.

We then investigated how pattern of vegetation community composition reflected in the NMDS ordination related to environmental and goose colony covariates of plot elevation (*Elev*), mean number of goose nests (*Nests*), number of years within the colony (*YrsIn*), and number of years since retraction of the colony (*YrsRet*) by vector overlays on the ordination using the function *envfit*. We used Pearson correlation coefficients between environmental and goose colony variables and NMDS scores to define the strength of correlations with ordination axes, with significance determined using 999 permutations.

We derived goose colony covariates of *Nests*, *YrsIn*, and *YrsRet* for each plot from long-term data (1966–2017: Alisauskas et al., 2012; Kerbes, 1994; Kerbes et al., 2006, 2014; McLandress, 1983; Ryder, 1970, 1971, 1972; R. Alisauskas, unpublished data). We calculated mean number of nests for each plot for 1991–2017 (1966–1990 data were not available); for plots observed to be outside the colony in all years, mean number of nests was set to zero. For plots recorded as in the colony for one or more years but calculated mean nest density was zero (as was the case for plots near the colony perimeter where nest density was extremely low), we set mean number of nests to 0.1. We calculated number of years within the colony and number of years since retraction of the colony perimeter for each sample plot from colony boundaries. The extent of the colony was monitored only periodically during 1966–1991 (1966, 1982, 1988, 1991), and so we interpolated the colony boundary over these short intervals. The extent of the nesting colony was unknown before 1966, and so the maximum number of years that a plot was within the colony was 52 years. We extracted elevation data for each plot from the Federal Geospatial Platform of Canada (<https://maps.canada.ca/>), and thus, these analyses contain information licensed under the Open Government Licence—Canada (<https://open.canada.ca/en/open-government-licence-canada>). We interpolated plot elevation (± 0.1 m) from the four nearest cells of these raster data with spatial resolution of 20 m.

Taxon richness of vegetation communities

We used linear models to investigate variation in vegetation taxon richness (*TaxonRich*, number of species or species groups detected) on sample plots in and near the nesting colony at Karrak Lake in 2017. We included in calculations of *TaxonRich* 10 rare species and species groups not listed in Table 1: foliose lichens, cup lichens,

mountain avens (*Dryas integrifolia*), moss campion (*Silene acaulis*), large-flowered wintergreen (*Pyrola grandiflora*), cloudberry (*Rubus chamaemorus*), louseworts (*Pedicularis* spp.), bog rosemary (*Andromeda polifolia*), bulblet saxifrage (*Saxifraga cernua*), and legumes (family Fabaceae). As well, we separated willows (a species group) into three growth forms for calculation of *TaxonRich*: dwarf, prostrate, and tall shrubs. We note that because we amalgamated some species into groups (i.e., species groups of graminoids, mosses, willows, and lichen growth form each contain multiple species), *TaxonRich* is an index of species richness, but one that is consistent across sampled plots. We used the same covariates described above (mean number of goose nests [*Nests*], number of years in the colony [*YrsIn*], number of years since retraction of the colony [*YrsRet*], and elevation [*Elev*]) as potential covariates to explain variation in *TaxonRich*. We examined Pearson's product-moment correlations among explanatory variables and excluded models with highly correlated covariates from the candidate set (*Nests* and *YrsIn*, see [Results](#)). We tested residuals of the most-parameterized models ($\{TaxonRich = Nests + YrsRet + Elev\}$ and $\{TaxonRich = YrsIn + YrsRet + Elev\}$ for normality and square-root-transformed dependent variables as required. We used Moran's *I* to measure the degree of spatial autocorrelation in both raw data and residuals from the most-parameterized models and employed spatial models if significant spatial autocorrelation existed. We report results of normality of residuals and spatial autocorrelation of most-parameterized models from model $\{TaxonRich = YrsIn + YrsRet + Elev\}$ for simplicity; results from model $\{TaxonRich = Nests + YrsRet + Elev\}$ were equivocal. We used corrected Akaike information criterion (AIC_c) for small sample sizes to examine the relative fit of each candidate model and incorporated model selection uncertainty by using a 90% confidence set of models (Akaike, 1973; Burnham & Anderson, 2002) from which we model-averaged slope estimates (and associated variances) of explanatory covariates.

State change in vegetation communities over a 16-year interval

We classified vegetation communities on sample plots with hierarchical cluster analysis employing Bray–Curtis distance (package *vegan*, Oksanen et al., 2019) using combined data for all plots sampled in 1998 and 2014 and assigned each plot in each year to a vegetation community class (hereafter, state). We compiled input data by summing point-intersect observations of each taxon per plot and included 14 taxa with either ~1% representation across all plots or those thought to indicate vegetation community change.

We fit multistate models implemented in Program MARK (White & Burnham, 1999) to model change in vegetation communities (i.e., probability of transition between states assigned by hierarchical cluster analysis) on sampled plots between 1998 and 2014, a 16-year interval. Multistate models allow estimation of probabilities of survival (S), recapture or detection (p), and transition among states (ψ). Our sample consisted of plots for which vegetation surveys were conducted in both 1998 and 2014; thus, both S and p were absolute, and we fixed these values to 1. We used the same covariates described for previous analyses (mean number of goose nests [$Nests$], number of years in the colony [$YrsIn$], and number of years since retraction of the colony [$YrsRet$] but instead calculated these covariates to 2014 rather than to 2017 as in previously described analyses) as potential covariates to account for variation in transition probabilities among states. We reasoned that these effects were likely to influence transition between states differently and so only included interactive models that involved these covariates in the candidate set of models.

Thus, the most general model was $\{S(=1) p(=1) \psi((v \times Nests) + (v \times YrsIn) + (v \times YrsRet))\}$, where both S and p were fixed at 1, and ψ varied interactively in response to vegetation state, v , and $Nests$, $YrsIn$, and $YrsRet$. Goodness-of-fit (GOF) can only be assessed on models without covariates so we conducted bootstrap GOF testing on model $\{S(=1) p(=1) \psi(v)\}$. The resulting estimate of variance inflation factor was $\hat{c} = 1.0$, so we used AIC_c (Akaike, 1973; Burnham & Anderson, 2002) to examine the relative fit of nine a priori candidate models to data. Our candidate set of models included all possible combinations for parameterizations of ψ . To aid in numerical convergence, particularly of more complicated models, we used initial parameter estimates (provided by model $\{S(=1) p(=1) \psi(v)\}$ to ensure that we determined the global (and not local) maxima. In the final candidate set of models, we retained the model of a given parameterization based on the best estimation (estimable SEs, correct number of parameters estimated). We used multinomial logit link function for ψ estimation so that transitions from a given state summed to 1.0 and based inference on effects of covariates with model-averaged slope estimates ($\hat{\beta}$) from a 90% confidence set of models.

RESULTS

Multivariate characterization of vegetation communities

We sampled 256 plots within and near the goose colony at Karrak Lake in 2017. Ordination of 17 species and

species groups accounting for 98.4% of point-intersect observations resulted in a three-dimensional solution capturing 24.1% of variation in the ranked distance matrix (Table 1, Figure 1). We used three axes for the final configuration because convergence was achieved easily (68–323 iterations over multiple attempts), reproducible (plots were very similar), with minimal stress (0.147) that was only slightly greater than an ordination using four axes (0.117). By comparison, ordination using only two axes did not achieve convergence after 1000 iterations and estimated stress was 0.195.

Elevation was most strongly correlated with the first axis of the 3-axis ordination, whereas the goose colony covariates were most strongly correlated with the second axis. Of greater interest and specifically, the second axis represented the covariates of number of years in colony ($YrsIn$, range: 0–52 years), mean number of goose nests ($Nests$, range: 0–31.7 nests), and time since retraction of the colony boundary ($YrsRet$, range: 0–17 years). Number of years in colony was strongly negatively correlated with the second axis (-0.944) but not with the first and third axes (0.071 and -0.322 , respectively, $r^2 = 0.324$, $p < 0.001$, Figure 1A; r^2 is the proportion of variation in the ordination explained by a particular variable). Likewise, $Nests$ was strongly negatively correlated with the second axis (-0.978) and not with the first or third axes (0.094 and -0.182 , respectively, $r^2 = 0.356$, $p < 0.001$, Figure 1B). $YrsRet$ was also correlated with the second axis (0.945) and not the first or third axes (-0.062 and 0.320, respectively, $r^2 = 0.080$, $p < 0.001$), but in the opposite direction to $YrsIn$ and $Nests$ (Figure 1C). Thus, positive values of axis 2 (NMDS2) characterized communities composed of species typically associated with habitats less disturbed by geese (Table 1, Figure 1). Elevation ($Elev$, range: 50–97 m asl) was more strongly correlated with the first axis (-0.789) than with the second or third axes (0.614 and -0.041 , respectively, $r^2 = 0.117$, $p < 0.001$, Figure 1D).

Taxon richness of vegetation communities

Taxon richness ($TaxonRich$) on 256 plots sampled in 2017 ranged between 1 and 14 taxa (species and species groups). Ranges of explanatory covariates were $YrsIn$: 0–52 years, $Nests$: 0–31.7 nests, $YrsRet$: 0–17 years, and $Elev$: 50–97 m asl. $Nests$ and $YrsIn$ were most highly correlated ($r = 0.603$, $p < 0.001$), so these effects were not included together in candidate models. All other correlations were $r < 0.3$. Thus, the resulting candidate set had 12 models, including an intercept-only model and all possible combinations of single effects. Transformation of $TaxonRich$ did not improve

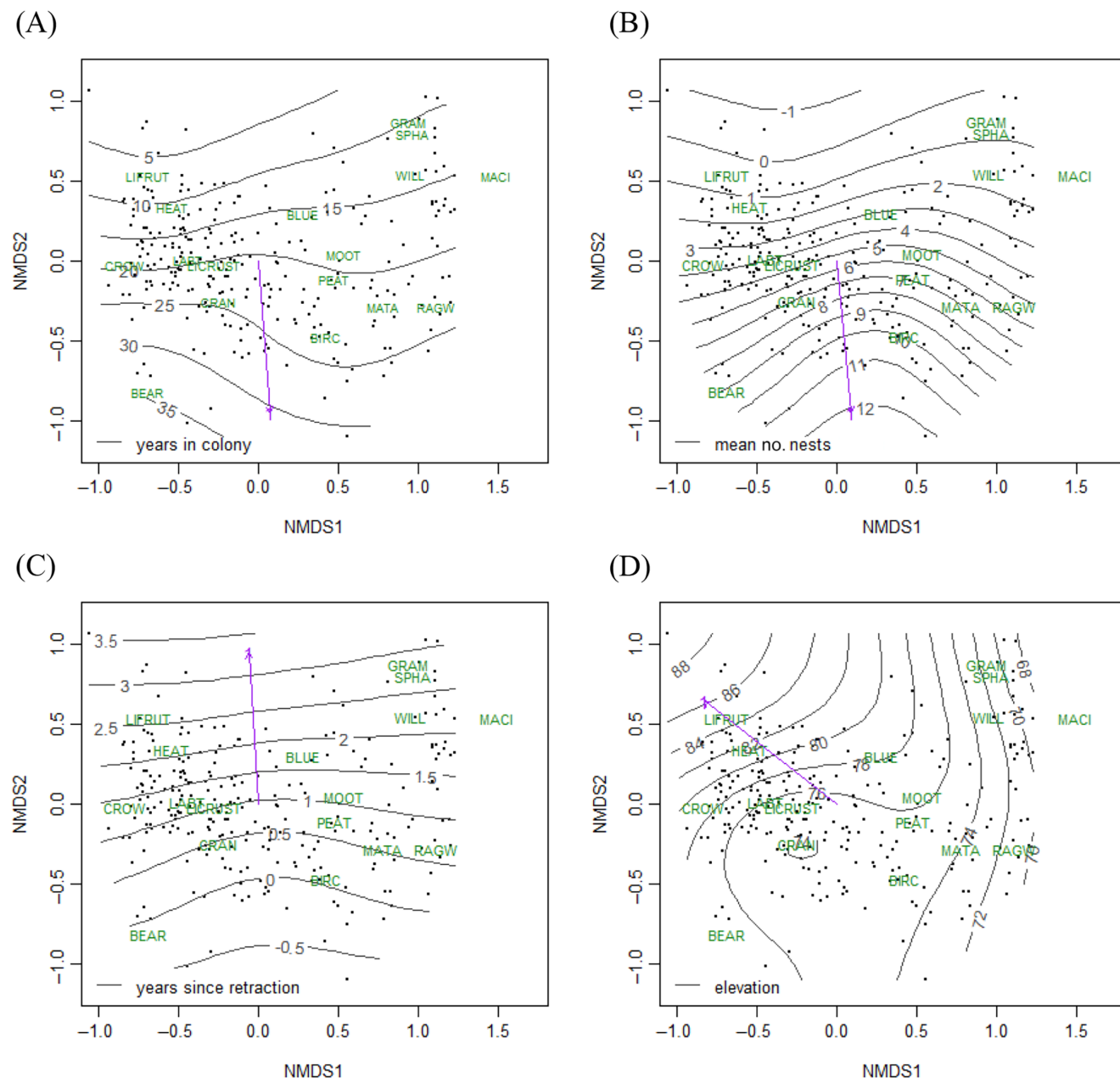


FIGURE 1 Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 17 vegetation taxa on 256 sample plots inside and near the snow and Ross's goose colony at Karrak Lake, Nunavut, in 2017. The three axes (third axis not shown) captured 24.1% of variation in the ranked matrix, with axes 1–3 capturing 14.2%, 6.0%, and 3.9% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlays (purple arrows) of environmental and biological covariates are depicted separately in each panel: (A) years in colony (*YrsIn*), (B) mean number of nests (*Nests*), (C) years since colony retraction (*YrsRet*), (D) elevation (*Elev*), with strength and direction of correlation given by the length of the vector line and vector arrow, respectively. Gray contour lines are also shown for each covariate. Species and species groups: BEAR, bearberry (*Arctous* spp.); BIRC, birch (*Betula glandulosa*); BLUE, blueberry (*Vaccinium uliginosum*); CRAN, cranberry (*Vaccinium vitis-idaea*); CROW, crowberry (*Empetrum nigrum*); GRAM, graminoids (grass and sedge spp.); HEAT, arctic heather (*Cassiope tetragona*); LABT, Labrador tea (*Ledum palustre*); LICRUST, lichen species with crustose growth form; LIFRUT, lichen species with fruticose growth form; MACI, marsh cinquefoil (*Comarum palustre*); MATA, mare's tail (*Hippuris vulgaris*); MOOT, moss species other than *Sphagnum* spp.; PEAT, dead moss species; RAGW, marsh ragwort (*Tephrosia palustris*); SPHA, *Sphagnum* spp.; WILL, willows (*Salix* spp.).

normality of residuals in the most-parameterized model ($W = 0.893$, $p < 0.001$ vs. $W = 0.985$, $p = 0.009$), so we analyzed untransformed values. Monte Carlo

simulation of Moran's I for *TaxonRich* indicated no spatial autocorrelation of raw data (Moran's $I = -0.035$, $p = 0.945$) or of residuals from the most-parameterized

model (Moran's $I = -0.040$, $p = 0.955$), so we did not employ spatial models in this analysis.

The 90% confidence set was composed of nine models that included effects of *Nests*, *YrsIn*, *YrsRet*, and *Elev* (Table 2). Taxon richness was higher for those areas with longer times since cessation of nesting, as the CI barely bounded zero ($\hat{\beta} = 0.073$ [95% CI: -0.004 , 0.149]) and was included in most of the top models of the confidence set. Model-averaged estimates of slopes for all other covariates included zero (*Elev*: -0.001 [-0.032 , 0.030]; *YrsIn*: -0.009 [-0.035 , 0.018]; *Nests*: 0.002 [-0.053 , 0.056]).

State change in vegetation communities over a 16-year interval

We classified 476 plots ($n_{1998} = 188$, $n_{2014} = 288$) in hierarchical cluster analysis and cut the resulting dendrogram to seven states and then visually inspected taxon means for each state (Table 3) to determine potential similarities among resulting states. We combined some states due to small sample size of some dendrogram states to reduce the number of transition probabilities, as follows. Of the seven states identified by cluster analysis, we

TABLE 2 Model selection results based on corrected Akaike information criterion (AIC_c) adjusted for sample size of taxon richness (number of species and species groups) on 256 sample plots at Karrak Lake, Nunavut, 2017.

Model	K	ΔAIC_c	ω_i
<i>YrsRet</i>	3	0.0	0.281
Intercept-only	2	1.7	0.118
<i>YrsIn</i> + <i>YrsRet</i>	4	1.8	0.112
<i>Nests</i> + <i>YrsRet</i>	4	2.0	0.102
<i>Elev</i> + <i>YrsRet</i>	4	2.0	0.102
<i>YrsIn</i>	3	2.7	0.075
<i>Nests</i>	3	3.7	0.045
<i>Elev</i>	3	3.7	0.045
<i>Elev</i> + <i>YrsIn</i> + <i>YrsRet</i>	5	3.9	0.041
<i>Elev</i> + <i>YrsRet</i> + <i>Nests</i>	5	4.1	0.037
<i>Elev</i> + <i>YrsIn</i>	4	4.7	0.027
<i>Elev</i> + <i>Nests</i>	4	5.7	0.017

Note: All candidate models are shown, but the first nine models constitute the 90% confidence set. Model variables are plot-specific and included number of years in the goose nesting colony (*YrsIn*), number of years since retraction of the colony (*YrsRet*), mean number of nests (*Nests*), and Elevation (*Elev*). Shown for each model are the number of parameters (K), difference in sample-size-corrected Akaike information criterion (AIC_c) relative to the top model (ΔAIC_c ; minimum value of the top model was 1110.2), and relative model weight (ω_i).

TABLE 3 Mean (1 SD) number of point-intersections (of possible 120) for each species or species group in upland (*UP*, $n = 241$ plots), graminoid (*GRAM*, $n = 89$ plots), and birch (*BIRCH*, $n = 146$ plots) states within and immediately outside of the snow and Ross's goose colony at Karrak Lake, Nunavut.

Species or species group	Habitat state		
	<i>UP</i>	<i>GRAM</i>	<i>BIRCH</i>
MOSS	7.6 (8.2)	31.3 (22.1)	16.2 (10.9)
GRAM	2.6 (4.8)	31.1 (22.1)	4.9 (7.7)
WILL	1.0 (2.3)	9.3 (11.4)	3.9 (5.7)
PEAT	2.9 (4.0)	9.2 (10.5)	20.8 (17.2)
CRAN	13.9 (10.7)	8.3 (7.6)	15.0 (9.8)
BIRC	4.3 (5.4)	7.7 (8.4)	22.3 (15.0)
LABT	22.3 (11.2)	6.5 (8.9)	13.0 (9.4)
LICH	23.3 (16.5)	3.5 (5.5)	3.9 (5.2)
HEAT	8.7 (6.9)	1.4 (3.6)	3.6 (5.2)
MACI	<0.1 (0.3)	1.0 (3.9)	0.5 (2.3)
BEAR	2.4 (4.9)	0.6 (1.8)	0.4 (1.3)
RAGW	0.1 (0.8)	0.5 (2.2)	1.5 (3.5)
CROW	1.4 (2.1)	0.3 (1.7)	0.6 (1.8)
MATA	<0.1 (0.4)	<0.1 (0.3)	0.7 (2.2)

Note: We determined state assignment by hierarchical cluster analysis of 476 plots sampled in 1998 and 2014. Data are presented from highest to lowest occurrence for the *GRAM* state.

Abbreviations: BEAR, bearberry (*Arctous* spp.); BIRC, birch (*Betula glandulosa*); CRAN, cranberry (*Vaccinium vitis-idaea*); CROW, crowberry (*Empetrum nigrum*); GRAM, graminoids (grass and sedge species); HEAT, arctic heather (*Cassiope tetragona*); LABT, Labrador tea (*Ledum palustre*); LICH, all lichen species; MACI, marsh cinquefoil (*Comarum palustre*); MATA, mare's tail (*Hippuris vulgaris*); MOSS, all moss species; PEAT, dead moss species; RAGW, marsh ragwort (*Tephrosia palustris*); WILL, willows (*Salix* spp.).

considered four (each with $n = 231$, 7, 1, and 2 plots) as upland (*UP*; we expressed states with italicized capitals to distinguish from non-italicized four-letter species codes). State *UP* was characterized by highest occurrence of lichens (LICH) and xeric species such as bearberry (BEAR, *Arctous* spp.) and crowberry (CROW, *Empetrum nigrum*), as well as high occurrence of Labrador tea (LABT, *Ledum palustre*), cranberry (CRAN, *Vaccinium vitis-idaea*), and white heather (HEAT, *Cassiope tetragona*) typical of both mesic and xeric habitats (Table 3). We considered two of seven states (each with $n = 43$ and 46 plots) as graminoid (*GRAM*). State *GRAM* exhibited highest occurrence of grasses and sedges (GRAM), mosses (MOSS, mainly *Sphagnum* spp.), and willows (WILL), all typically occurring in hydric to mesic habitats (Table 3). We classified the remaining 146 plots as a state represented by birch (*BIRCH*), as these plots were characterized by highest incidence of birch (BIRC,

Betula glandulosa) with the presence of exposed peat (PEAT), CRAN, and LABT (Table 3). We then used these resulting states of *UP*, *GRAM*, and *BIRCH* in multistate modeling.

Individual covariates associated with 156 paired plots (sampled in both 1998 and 2014) ranged from *Nests* (0–34.5 nests), *YrsIn* (0–49 years), and *YrsRet* (0–14 years). The top two models (combined weight of 0.994) of transition probability among habitat states contained covariates *Nests* and *YrsIn* (Table 4). Model-averaged slope estimates from these two models suggested that probability of state transition from *GRAM* to *UP* and from *GRAM* to *BIRCH* over this 16-year period was directly related to *Nests* ($\hat{\beta}_{Nests \times GRAM \rightarrow UP}$: 0.740 [95% CI: 0.141, 1.340]; $\hat{\beta}_{Nests \times GRAM \rightarrow BIRCH}$: 0.904 [0.328, 1.481]); all other 95% CI of slope values for *Nests* included zero. All 95% CI of slope estimates for influence of *YrsIn* on transition probabilities among habitats included zero.

Transition probabilities varied among states, and estimates from model $\{S(=1) p(=1) \psi(v)\}$ (without effects of covariates) were highest for *GRAM*; of 47 plots classified as *GRAM* in 1998, only eight plots persisted as *GRAM* in 2014, and sum of transition probabilities to a different state ($\psi_{GRAM \rightarrow BIRCH} = 0.723$ [95% CI: 0.580, 0.832], $\psi_{GRAM \rightarrow UP} = 0.106$ [0.045, 0.231]) was 0.829. Of 24 plots classified as *BIRCH* in 1998, 19 remained as *BIRCH* in 2014, with a sum of transition probabilities to a different state

($\psi_{BIRCH \rightarrow GRAM} = 0.042$ [0.006, 0.244], $\psi_{BIRCH \rightarrow UP} = 0.167$ [0.064, 0.369]) of 0.209. Of 85 plots classified as *UP* in 1998, 65 remained as *UP* in 2014, with a sum of transition probabilities to a different state ($\psi_{UP \rightarrow BIRCH} = 0.212$ [0.138, 0.311], $\psi_{UP \rightarrow GRAM} = 0.024$ [0.006, 0.089]) of 0.236.

DISCUSSION

Exposed peat in arctic regions can result from hydrological fluctuations by drawdown in lowland areas and under abnormally dry conditions in upland areas (Didiuk & Ferguson, 2005), whereas bare mineral sediment is common in tidal areas along coasts and along rivers from solifluction (Conkin & Alisauskas, 2017). However, ornithogenic effects of foraging and nesting by high densities of light geese resulted in substantial increase of exposed peat in mesic and hydric habitats (Conkin & Alisauskas, 2017) and exposed mineral soil in xeric habitats (Alisauskas et al., 2006). This study supports those conclusions and also demonstrated previously unreported shifts in community composition of arctic plant communities in upland and lowland habitats within the large nesting colony at Karrak Lake due to these ornithogenic effects, as well as reversals from removal of these same effects.

Lowland and upland community change at the Karrak Lake nesting colony

Plant communities vary along abiotic gradients such as topography, moisture, and soil properties (Gough et al., 2000; Jones & Henry, 2003; McNaughton, 1983). In addition to heterogeneity of plant communities imposed by abiotic gradients (e.g., elevation), we detected pronounced shifts in community structure within the nesting colony at Karrak Lake due to variation in intensity and duration of use by light geese. Compared with lowland areas outside of colonies that face foraging pressure from transient flocks throughout the snow-free season (that is, by pre- and failed-breeding geese, as well as post-hatch individuals with goslings), light geese continually occupy and intensely use nesting colonies at high densities for longer durations: birds initiate nesting shortly after arrival to colonies and remain there for approximate 30-day laying and incubation periods, leaving colonies shortly after hatch (Jónsson et al., 2020; Mowbray et al., 2020). Much of this occupancy occurs before the growth of aboveground production, placing disproportionate foraging pressure on belowground plant biomass. Combined effects of uprooting of vegetation for nest construction (Alisauskas et al., 2006; McCracken

TABLE 4 Candidate model set for transition probabilities (ψ) among upland (*UP*), graminoid (*GRAM*), and birch (*BIRCH*) states between 1998 and 2014 on 156 sample plots within and immediately outside of the snow and Ross's goose colony at Karrak Lake, Nunavut.

Model	K	ΔAIC_c	ω_i
$S(1) p(1) \psi((v \times Nests))$	12	0.0	0.581
$S(1) p(1) \psi((v \times Nests) + (v \times YrsIn))$	18	0.7	0.413
$S(1) p(1) \psi((v \times Nests) + (v \times YrsRet))$	18	11.9	0.001
$S(1) p(1) \psi((v \times YrsIn) + (v \times YrsRet))$	18	12.1	0.001
$S(1) p(1) \psi((v \times Nests) + (v \times YrsIn) + (v \times YrsRet))$	24	12.2	0.001
$S(1) p(1) \psi(v)$	6	13.0	0.001
$S(1) p(1) \psi((v \times YrsRet))$	12	13.5	0.001
$S(1) p(1) \psi((v \times YrsIn))$	12	16.9	0.000
$S(.) p(.) \psi(.)$	2	96.4	0.000

Note: Parameters estimated were transition between *UP*, *GRAM*, and *BIRCH* states, while survival (*S*) and detection probability (*p*) were fixed at 1. Model variables include state (*v*), number of years in the goose nesting colony (*YrsIn*), number of years since retraction of the colony (*YrsRet*), and mean number of nests (*Nests*). Shown for each model are the number of parameters (*K*), difference in sample-size-corrected Akaike information criterion (AIC_c) relative to the top model (ΔAIC_c ; minimum value of the top model was 207.6), and relative model weight (ω_i).

et al., 1997) and foraging during the nesting period changed the community composition of both upland and lowland communities.

In upland habitats, fruticose lichens, crowberry, and white heather were generally more abundant at low levels of disturbance. Geese incorporated lichens into nests (McCracken et al., 1997; D. Kellett, personal observation), and lichen species are particularly sensitive to trampling (Cooper et al., 2001; Manseau et al., 1996). At high levels of disturbance, crustose lichens and bearberry were more common. Crustose lichens readily colonize bare substrate (Belnap et al., 2001), and their presence is likely an indicator of exposed mineral soil resulting from vegetation removal and perhaps erosion of exposed peat in upland habitats. Bearberry forms a dense, prostrate mat (Aiken et al., 2007), and whole plants (but occasionally leaves) are rarely used in nest construction (McCracken et al., 1997; D. Kellett, personal observation), suggesting it is less easily uprooted. Cranberry and Labrador tea are widespread throughout the colony and occur within a wide range of elevations but may also thrive in disturbed habitats (Manseau et al., 1996). As well, Conkin and Alisauskas (2017) reported conversion of upland habitats to exposed peat within nesting colonies. Our multivariate analyses placed exposed peat in an intermediate position on the NMDS axis most correlated with elevation, supporting observations of exposed peat in upland as well as lowland areas. Also, we estimated transition probability of 0.212 from upland to birch states. The birch state contained substantial exposed peat, suggesting that conversion of disturbed upland plant communities to those containing exposed peat also occurred.

Disturbance to graminoid-dominated grazing lawns in lowland habitats within the nesting colony by foraging and nesting light geese resulted in an obvious and consistent shift in plant community composition. At low levels of disturbance, NMDS ordinations demonstrated that graminoid, *Sphagnum*, and willow species dominated lowland communities. In areas subjected to intense and long-term nesting, altered lowland plant communities contained high incidence of peat, birch, non-*Sphagnum* moss species, marsh ragwort, and mare's tail (*Hippuris vulgaris*), consistent with observations by earlier investigations (Abraham et al., 2020; Alisauskas et al., 2006; Conkin & Alisauskas, 2017; Fontaine & Mallory, 2011; Kerbes et al., 1990). Non-*Sphagnum* mosses ("moss carpets," sensu Fontaine & Mallory, 2011; Kotanen & Jefferies, 1997), marsh ragwort, and marsh cinquefoil were previously identified as colonizers of northern freshwater plant communities disturbed by light geese (Alisauskas et al., 2006; Fontaine & Mallory, 2011; Kerbes et al., 1990; Kotanen & Jefferies, 1997). We did not clearly identify marsh cinquefoil as a colonizer of

disturbed habitats; at Karrak Lake, this species existed in intermediary positions on the NMDS axis correlated with disturbance by light geese and generally occurred in more hydric conditions. Foraging by geese may speed desiccation of low-lying areas by increasing the rate of evaporation following removal of vegetation (Conkin & Alisauskas, 2017), and marsh ragwort appears to thrive in such conditions (D. Kellett, personal observation). In deeper basins where standing water remains, mare's tail colonized disturbed lowland areas at Karrak Lake presumably formerly inhabited by graminoid species in wet sedge meadows (D. Kellett, personal observation).

Overwhelmingly, however, birch was the most abundant species in altered vegetation communities at lower elevations. As well, we estimated high transition probability (0.723 over a 16-year period) of graminoid-dominated to birch-dominated communities within the nesting colony. Conversion of upland to birch states also occurred within this same period, but less frequently (transition probability of 0.212). Further, Conkin and Alisauskas (2017) reported conversion of wet sedge meadows to low shrub and shrub thicket (primarily birch and willow species), albeit at lower levels, over a broader area within the Sanctuary. Expansion of shrubs resulting from climate warming (Beamish et al., 2020; Elmendorf et al., 2012; Myers-Smith et al., 2011) likely at least partially explains the increase in birch observed in this study. Paradoxically, herbivory generally mitigates increased dominance of shrubs facilitated by climate warming (Leffler et al., 2019; Myers-Smith et al., 2011, but see Carlson et al., 2018; Post et al., 2020). However, geese do not consume birch or willows (Gloutney et al., 2001; Kerbes et al., 1990) nor are these woody plants easily uprooted for nest construction (D. Kellett, personal observation). Birch was more prevalent in heavily used areas such as nesting colonies compared with brood-rearing regions (Kellett, 2021), suggesting that intense and long-term disturbance by light geese may function additively with climate change to accelerate birch encroachment. Shrub encroachment facilitated by climate change is most pronounced in warmer subarctic regions without permafrost or with discontinuous permafrost (Beamish et al., 2020; Elmendorf et al., 2012; Sturm et al., 2005), but intense foraging of graminoids results in soil warming (Myers-Smith et al., 2011) and may hasten shrub encroachment in this colder arctic region. As well, birch responds to nutrient inputs (Chapin & Shaver, 1985; Myers-Smith et al., 2011), allowing this species to increase in goose-fertilized disturbed areas without competition from graminoids for nutrients, moisture, or space. Once established, growth of birch may benefit from positive feedback involving increased snow accumulation, which provides insulation, moisture, and microbial-sourced nutrients, as well as

reduced shearing of branches by winter winds and frost damage (Sturm et al., 2005; Myers-Smith et al., 2011), leading to further growth and establishment.

Foraging and nesting light geese had little impact on taxon richness of vegetation communities within the nesting colony. Although community composition of vegetation communities shifted to altered states, particularly at lower elevations, long-term occupancy by nesting light geese did not result in dominance by a limited number of species or complete eradication of certain species, at least within the range of occupancy experienced at Karrak Lake to date (but see Alisauskas et al., 2006). This contrasts with conditions along the west coast of Hudson Bay, in which long-term and intense occupancy by transient and nesting geese reduced plant species richness (Handa et al., 2002).

We found weak evidence for increase in taxon richness in areas that experienced retraction of the nesting colony, suggesting that cessation of grazing and nesting pressure results in rapid reestablishment by nearly eradicated plant species, particularly graminoids. That is, plant species targeted by nesting and foraging geese persist at low abundance in intensively used areas, but are not completely eliminated, and thus reestablish when nesting and foraging pressure decline. We acknowledge the limitation of assigning species to species groups (taxa) and suggest that future research strives to determine species of graminoids, willows, lichens, and mosses during vegetation surveys to investigate how true plant species richness and succession among and within plant taxa or functional groups (e.g., graminoids) responds to release from grazing and nesting pressure by light geese.

Existence of alternative stable states?

Alternative stable states are relatively resistant to change but can exhibit rapid shifts to another state if forced (van der Wal, 2006). Expressed differently (Beisner et al., 2003), a plant community in an alternative stable state returns to the same configuration after a small perturbation (e.g., optimal grazing of aboveground plant biomass), but may shift to a different equilibrium after a large perturbation (e.g., cumulative effects of intense grazing, grubbing, shoot-pulling, and nest construction). An alternative stable state of bare sediment in subarctic coastal regions that initially resulted from intense grazing by light geese can be maintained by positive feedback between soil salinity and plant regeneration, with the result that reestablishment of plant communities can be delayed even after complete cessation of grazing pressure (Abraham et al., 2005; Jefferies & Rockwell, 2002; McLaren & Jefferies, 2004; Srivastava & Jefferies, 1996).

Kellett and Alisauskas (2022) provided evidence that heavily grazed plant communities have the potential to revert to former states upon cessation of intense grazing and nesting pressure. In this study, we observed an increase in taxon richness upon cessation of nesting pressure. As such, we suggest that altered communities are likely not alternative stable states in this ecosystem. However, we are not confident that all birch-dominated communities will readily revert to former graminoid-dominated or upland communities and suggest that research over a longer time series is required to determine eventual outcomes. Depending on the extent to which birch becomes dominant, it may become an alternative stable state in arctic inland regions, due to potential positive feedback between birch growth and establishment and snow catchment, as well as its unpalatability to geese and potential ability to out-compete graminoids for space, water, and nutrients. That is, once birch is established, it may become self-sustaining and continue to persist when its dominance reaches a threshold, and geese no longer forage there due to extirpation of graminoids. In this manner, birch-dominated communities may represent an alternative stable state, until other ecological factors perhaps such as fire or a series of winters with little snow cover and high wind lead to its decline (Beamish et al., 2020). We suggest that future research may require continued measurement from a multidecadal perspective to test the hypothesis that birch-dominated communities represent an alternative stable state. The persistence of birch communities after cessation of intense foraging and nesting by light geese, which likely facilitated the ability of birch to establish and is at least partly responsible for its creation (Beisner et al., 2003), remains to be determined through repeated vegetation monitoring of formerly occupied habitats.

CONCLUSIONS

We demonstrated changes to community composition of arctic vegetation communities in response to herbivory and nesting by light geese within a landscape mosaic of terrestrial plant communities. These effects of herbivory and nest construction were not uniform across this widespread nesting colony and, together with influence of abiotic gradients, created a heterogeneous mosaic of vegetation communities. Light geese can dramatically alter ecosystem structure and might appropriately be considered as “ecosystem engineers” in this light.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kellett & Alisauskas, 2024) are available from Dryad: <https://doi.org/10.5061/dryad.rjdfn2zn0>.

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