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Tundra Vegetation Change near Barrow, Alaska (1972–2010)

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Abstract
Knowledge of how arctic plant communities will respond to change has been largely derived from plot level experimental manipulation, not from trends of decade time scale environmental observations. This study documents plant community change in 330 marked plots at 33 sites established during the International Biological Program near Barrow, Alaska in 1972. Plots were resampled in 1999, 2008 and 2010 for species cover and presence. Cluster analysis identified nine plant communities in 1972. Non-metric multidimensional scaling (NMS) indicates that plant communities have changed in different ways over time, and that wet communities have changed more than dry communities. The relative cover of lichens increased over time, while the response of other plant functional groups varied. Species richness and diversity also increased over time. The most dramatic changes in the cover of bryophytes, graminoids and bare ground coincided with a lemming high in 2008.

Keywords: arctic tundra, climate change, plant community change, plant diversity, herbivory, ecosystem change

S Online supplementary data available from stacks.iop.org/ERL/7/015508/mmedia

1. Introduction

Climate warming is pronounced at high northern latitudes (ACIA 2005, Serreze 2010). Time series analysis of satellite remote sensing between 1982 and 2008 suggests that there has been a greening of arctic landscapes with the most evident changes occurring where there has been summer warming of coastal tundra adjacent to regions of high sea ice loss (Bhatt *et al* 2010). Changes in ecosystem properties underpinning this greening trend remain poorly quantified (Callaghan *et al* 2011b). Although some observational studies document vegetation change commensurate with warming, such as shrub expansion (Tape *et al* 2006) and treeline advancement (Lloyd 2005, Danby and Hik 2007), there is a general scarcity of ground-based studies that examine vegetation change in the Arctic over decade time scales. Experimental studies, however, suggest that some plant species respond to warming physiologically (Hobbie and Chapin 1998, Hudson *et al* 2011), and phenologically (Arft *et al* 1999, Klady *et al* 2011), and that these responses may manifest to plant community change (Walker *et al* 2006).

Tundra landscapes have high levels of spatial heterogeneity and temporal variability (Epstein *et al* 2004), making the evaluation of long-term vegetation change difficult to detect. In part, this is a result of the fine scale heterogeneity of tundra landscapes that influences soil moisture, nutrient availability and seasonal permafrost thaw, for example. This heterogeneity often occurs over short distances (<1 m)

and serves as an important control of plant community structure and diversity (Webber 1978). Interannual variability in climate and herbivory can also affect plant productivity and reproduction (Chapin *et al* 1987, Walker *et al* 1995, Johnson *et al* 2011). In particular, lemmings can remove or destroy as much as 90% of above ground vegetation during winter seasons (Stenseth and Ims 1993). Like other factors controlling plant and ecosystem structure and function in the Arctic, the role lemmings play in controlling vegetation structure and function over decadal time scales is poorly resolved due to a lack of sufficient time series data collected at all phases of a lemming population cycle (Ims and Fuglei 2005, Pitelka and Batzli 2007).

Detecting change in the structure of arctic tundra has significant implications for understanding ecosystem functional responses to arctic change. Different plant communities have different ecosystem functional properties (e.g. carbon balance and surface energy budget, Shaver and Chapin 1991, Chapin *et al* 2005, Oberbauer *et al* 2007), and a change in the spatial extent of different plant communities or changes in plant species composition and morphology could alter landscape to regional scale fluxes of carbon and surface energy budgets (Strom and Christensen 2007, Sullivan *et al* 2008). Of primary concern is a scenario that could lead to the substantial soil organic carbon pool in the Arctic (Tarnocai *et al* 2009) being mobilized to a greenhouse active state in the atmosphere or a change in vegetation structure, such as an increase in shrub density, which could alter surface energy balance (Chapin *et al* 2005). Both scenarios appear to have the capacity to alter regional to global carbon balance and radiative forcing potential (Schuur *et al* 2008).

Remotely detected changes in the normalized difference vegetation index (NDVI) of the arctic coastal plain near Barrow, Alaska appear to be among the most dramatic recorded for much of the Arctic (Bhatt *et al* 2010). Factors such as air temperature, soil moisture and snow cover, which control plant species composition and plant community distribution in the Barrow area (Webber *et al* 1980), are changing (Stone *et al* 2002, Hinzman *et al* 2005), but evidence of vegetation change supporting widespread greening in the Barrow area has not been reported. Experimental warming studies associated with the International Tundra Experiment (ITEX) near Barrow suggest plant phenology and plant community composition, structure and biomass respond to moderate warming of surface air (Hollister *et al* 2005a, 2005b, Hollister and Flaherty 2010). Species diversity has also declined in response to experimental warming, which is similar to trends reported in other manipulative warming studies throughout the Arctic (Chapin *et al* 1995, Molau and Alatalo 1998, Walker *et al* 2006). Although Hollister *et al* (2005b) documented changes in species diversity within ITEX control plots between 1994 and 2000, few other studies have reported findings that could otherwise explain the dramatic greening trends documented from satellite imagery for the northern Arctic Coastal Plain in Alaska (Bhatt *et al* 2010).

This study documents the rescue and resampling of 33 sites originally established in 1971 near Barrow as part of the International Biological Program (IBP). These sites were originally used with 10 other sites that have since been disturbed or remain difficult to precisely relocate to describe plant community composition and distribution in the Barrow area (Webber 1978). Specifically, we compare plant community composition data collected in 1972 with data from resampling efforts that took place in 1999, 2008 and 2010 to determine how vegetation has changed over time by assessing: (i) the direction and magnitude of vegetation change and how this varies for different plant communities, (ii) how changes in different plant functional groups are underpinning plant community change, (iii) how plant species richness and diversity have changed over time, and (iv) how the abundance of individual species has changed. A companion study (Lara *et al* 2012) reports on the consequences of plant community change documented herein on ecosystem function. This study is a contribution to the International Polar Year-Back to The Future (IPY-BTF) project (IPY #512), which aimed to determine the impacts of arctic plant community change on ecosystem function over decadal time scales by revisiting and resampling historic research sites more than 25 years in age (Callaghan *et al* 2011a).

2. Methodology

2.1. Study area

The IBP study area was active between 1970 and 1973, and focused on a study area near Barrow, Alaska at the northernmost point on the Alaskan Coastal Plain (71°18′N 156°40′W) in close proximity to both the Chukchi and Beaufort Seas. Common landscape features include ponds, vegetated drained lake basins, low-gradient streams, hummock slopes, high and low-centered polygonal tundra, and meadows (Webber *et al* 1980). Floristic diversity near Barrow (ca. 120 species, Murray and Murray 1978) is low relative to the 574 vascular plant species recorded on the North Slope of Alaska (Webber 1978). As a contribution to the IBP, Webber (1978) described eight plant communities comprised of similar dominant species that differed in their abundance between communities. The distribution of plant communities near Barrow is primarily controlled by soil moisture, soil anaerobicity, soil phosphate and snow cover (Webber *et al* 1980). Soils are poorly drained throughout the snow free period (June through September) and active layer depth rarely exceeds 40 cm (Hinkel and Nelson 2003).Various forms of natural and anthropogenic disturbance are active in the region. The most abundant herbivore is the brown lemming, which has population outbreaks exceeding 200 ha^{-1} approximately every 3–5 years (Batzli *et al* 1980). Other vertebrate herbivores are largely absent from the IBP area, likely due to the close proximity to the City of Barrow. The urban fringe of Barrow has developed toward the study site and now two gravel roads transect the IBP where there is also evidence of occasional off road vehicle use. The study area is likely to have undergone subtle but sustained drying with the increased hydraulic gradient caused by the draining of Middle Salt Lagoon and Footprint and Dry Lakes in 1950 and the gradual headward erosion of Footprint Creek since this time (Brown 1980).

Table 1. Change in mean species richness and Shannon index of diversity between each sampling interval for each plant community (* significant increase or decrease, $p < 0.05$). Communities were sampled in 1972, 1999, 2008 and 2010 near Barrow, Alaska.

	1972–1999	1972–2008	1972–2010	1999–2008	1999–2010	2008–2010
			Species richness			
ACG	−1.64*	−1.55*	−0.94	0.09	0.70	0.60
CAG	1.80	1.75	2.30*	−0.05	0.50	0.55
PAG	1.60	1.20	1.40	−0.40	−0.20	0.20
FG	−1.88*	1.40	2.68*	3.28*	4.55*	1.28*
WG	−2.43*	−1.56*	−0.38	0.87	2.05*	1.17*
MG	−0.45	0.87	3.08*	1.32	3.53*	2.22*
DMSG	−1.65	−0.45	0.45	1.20	2.10	0.90
DSG	−0.03	0.53	4.40*	0.57	4.43*	3.87*
SDSG	1.73	2.18	4.27*	0.45	2.55	2.09
All	−1.09*	−0.09	1.38*	1.00*	2.48*	1.48*
			Shannon index			
ACG	−0.20	−0.34*	−0.23*	−0.14	−0.03	0.11
CAG	−0.08	0.03	0.12	0.12	0.20	0.09
PAG	0.54*	0.34*	0.39*	−0.20	−0.15	0.05
FG	−0.13	0.15*	0.23*	0.28	0.36	0.08
WG	−0.19*	−0.21*	−0.10*	−0.02	0.09	0.11*
MG	0.02	0.08	0.28*	0.06	0.27*	0.21*
DMSG	−0.04	0.00	0.14	0.04	0.18	0.14
DSG	0.04	0.09	0.31*	0.05	0.27*	0.22*
SDSG	0.07	0.04	0.23	−0.02	0.16	0.19
All	−0.08*	−0.06*	0.08*	0.03	0.16*	013*

2.2. Vegetation sampling

Forty three vegetation sites (hereafter called historic sites) in the IBP study area were established in 1971 after being chosen for their characteristic representation of the vegetation in the Barrow area. The sites were first sampled in 1972 and then relocated in 1998. Thirty three sites were found to be intact and were resampled in 1999, 2008 and 2010 using the same method Webber employed at the first sampling in 1972. Most sites measured 1 m × 10 m and consisted of ten contiguous 1 m² plots (330 total). The exceptions to this are 15 irregularly shaped sites with ten randomly chosen non-contiguous 1 m² plots in sites where ecosystem functional studies were performed prior to Webber's 1972 plant community study. We estimated per cent cover for all vascular and lichen species within a 10 cm × 100 cm strip along one edge of each 1 m² plot (bryophytes were lumped as a single record for all bryophytes within a plot to be consistent with the sampling methodology used in 1972). Species that occurred outside the strip but within a plot were recorded as present. Plots were sampled close to peak growing season between mid July and early August. A range of ecosystem functional data were collected in close proximity to these study plots and are reported by Lara *et al* (2012). Soil moisture and thaw depth measurements were taken at each plot using a time domain reflectometer probe and a metal probe respectively and are reported in detail by Lara *et al* (2012).

2.3. Data analysis

We calculated relative cover for each species and non-biological category (e.g. bare ground, litter) in every 1 m²

plot by multiplying cover estimates by 100 and dividing by the total cover of all species and non-biological categories in the plot. Relative presence was calculated by multiplying presence by 100 and dividing by the total species richness of each plot. We then summed relative cover and relative presence and divided this by 2 to obtain a cover index for each species and category in every plot (*sensu* Webber 1978). Hereafter, this index is referred to as a species index. Species index values ($n = 75$ species) were used to classify the original plots sampled in 1972 ($n = 430$ plots) into discrete plant communities using Hierarchical Cluster Analysis in PC-ORD 5.10 (MjM Software Design Gleneden Beach, OR, USA). Sørensen's similarity coefficient was used with a flexible beta linkage method ($\beta = -0.25$) to minimize chaining (McCune and Grace 2002). A cutoff of less than 50% similarity was used to match our plant community classification with a regional supervised land cover classification produced by Tweedie *et al* (2012). Sub-communities were created where a group not identified by the regional land cover classification clustered within the per cent cutoff range. Acronyms were assigned for each community as described below. Indicator species analysis was performed using PC-ORD following Dufrene and Legendre (1997) with a randomized approach to test for significance. The five species with the highest indicator value in each plant community are reported in supplementary documentation (available at stacks.iop.org/ERL/7/015508/mmedia).

We used non-metric multidimensional scaling (NMS) to ordinate all plots for all sampling years in PC-ORD using a Sørensen (Bray–Curtis) similarity coefficient, a random starting configuration, and 250 runs with randomized and real data. Dimensionality and stress were determined by PC-ORD and to aid visualization, axes scores for each
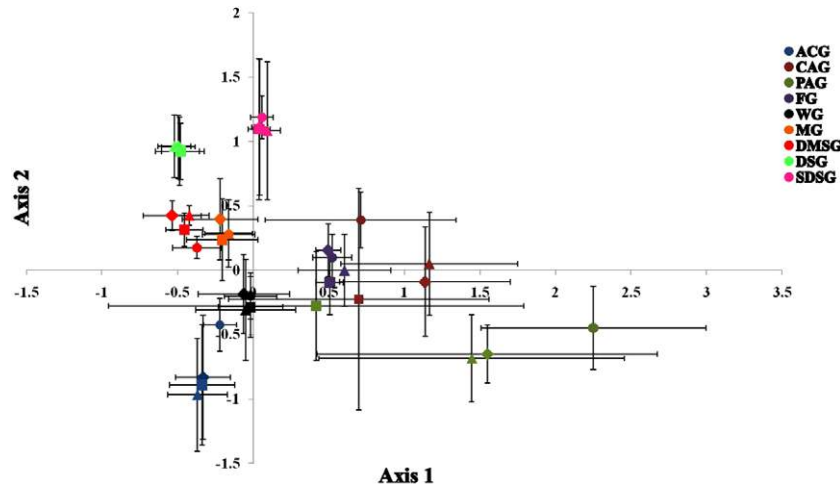
Figure 1. Non-metric multidimensional scaling ordination of all plant communities for all years sampled (1972, 1999, 2008, 2010) in the coastal tundra near Barrow, Alaska. Points represent the mean NMS axis scores for all plots classified in a given plant community in a given sampling year. Sampling times are represented by different shapes (1972—circle, 1999—diamond, 2008—square, 2010—triangle). Axis 1 was most strongly correlated with thaw depth ($r^2 = 0.326$), and axis 2 was most strongly correlated with soil moisture ($r^2 = 0.839$).

plot were averaged by plant community derived from the cluster analysis (figure 1). An index of net change for each plant community was determined by summing the absolute differences in axis scores between the three inter-sampling periods (1972–1999, 1999–2008 and 2008–2010). The magnitude of plant community change over time was assessed by running an additional NMS ordination of all data in PC-ORD with plot data arranged chronologically by year and with standardized plot names for each sampling time. The successional vector representing change through time for each plot was calculated using trigonometry to compute the hypotenuse length between successive axes scores in the ordination. Hypotenuse lengths were normalized by the number of years within a given sampling interval, and then averaged for each plant community and log-transformed. After reviewing preliminary results, the most dramatic changes in plant communities appeared to correspond to lemming population outbreaks. In order to ascertain the likely impact of herbivory on plant community change, we plotted the mean vector lengths against the time since a lemming population outbreak within a given sampling period. Sampling in 2008 was the only sampling time that coincided with a lemming population high and the sampling in 1972 and 2010 were one and two years following lemming population outbreaks respectively. Long-term plant community change was assessed by determining trajectories of change over the 1972–2010 sampling interval.

Relative cover of bare ground, litter and plant functional groups were calculated following the method of Chapin and Shaver (1996), and analyzed using a multivariate analysis of variance (MANOVA) in JMP 9.0 (SAS Institute Cary, NC, USA) to test differences in the relative cover of functional groups in each community at a given sampling time. Wilk's λ was used to determine if each functional group varied between sampling times and among plant communities at different sampling times (sampling time ∗ plant community). Species richness and Shannon's index of diversity were calculated in PC-ORD for each plot for each sampling time using species

cover values averaged by plant community. To determine how species richness and Shannon's index of diversity varied among plant communities through time, we used a repeated measure ANOVA in JMP 9.0 with plant community as the within subject factor. If Wilk's λ statistic for either time, or time by plant community interaction resulted in a probability less than 0.05, differences between communities and sampling dates were tested using least significant difference (LSD) tests of the univariate analysis of variance (ANOVA) within the repeated measures.

To determine how the relative abundance of these species differed between sampling times, we assumed the data fit a Poisson distribution and performed a general linear model in JMP 9.0 with a log-link function using a Firth Adjusted Maximum Likelihood to estimate parameters. This approach was chosen due to the lack of uniformity for all species among plant communities that resulted in strongly non-normal datasets for individual species. We applied a separate general linear model for each species using plant community and sample date as factors, and determined significance for that species and plant community if the probability of the resulting X^2 for the plant community ∗ sample date interaction was below 0.1. We also determined if the cover of each species was different between sampling dates across all plots if the probability of the X^2 for sample date was less than 0.1.

3. Results

3.1. Plant community change

Cluster analysis of the original 430 plots sampled by Webber in 1972 yielded nine plant communities (see supplementary document 1 for community descriptions available at stacks. iop.org/ERL/7/015508/mmedia). Wet graminoid tundra (WG) and moist graminoid tundra (MG) had the highest number of plots, while pond *Arctophila* graminoid tundra (PAG) and successional dry-dwarf shrub-graminoid tundra (SDSG) had

the lowest with only one site located in each plant community (10 plots each). Other communities identified by the cluster analysis include: aquatic *Carex* graminoid tundra (ACG), creek *Arctophila* graminoid tundra (CAG), seasonally flooded graminoid tundra (FG), dry-moist dwarf shrub-graminoid tundra (DMSG), and dry-dwarf shrub-graminoid tundra (DSG). The NMS ordination of all plots and sample times recommended a two-dimensional solution and had a final stress of 23.43 that is typical for large datasets (McCune and Grace 2002). Instability was 0.00367 after 500 iterations and the proportion of the variance explained by the ordination represented 79% of the cumulative variance with axis one and two representing 30.6% and 48.4% respectively. Axis one correlated most strongly with thaw depth ($r^2 = 0.326$), while axis two correlated well with soil moisture ($r^2 = 0.839$). Generally, wet and aquatic communities were more dynamic between sampling times than dry and moist community types (figure 1). Plots associated with each of the classified plant communities showed no sustained change trajectory along either axis. Mean axis scores for each plant community were within one standard deviation of each other at each sampling time. The greatest community change was detected after a two year period following a lemming outbreak (2008–2010, average vector length = 0.20) (supplementary document 2 available at stacks.iop.org/ERL/7/015508/mmedia), while the least change was detected over the long-term 1972–2010 change trajectory (0.01).

3.2. Change in plant functional groups

The relative cover of all plant functional groups was significantly different (MANOVA, $p < 0.05$, Wilk's $\lambda = 0.27$) among the four sampling times with the exception of shrubs (numerator DF = 5, denominator DF = 1312). Additionally, functional group relative cover varied significantly among different plant communities and sampling times with the exception of forbs, lichens and shrubs (numerator DF = 15, denominator DF = 1312). Though shrub cover differed among various communities, no overarching change over time was documented (figure 2). Overall, lichen cover increased through time. Cover for forbs, graminoids, litter and bryophytes appeared to vary considerably among sampling times. The relative cover of bryophytes was highest in 1972 (26.5%, figure 2 All), while lichen and shrub cover was lowest (5.2% and 4.2%, respectively). Graminoid cover was greatest (39.8%) and forbs lowest (6.5%) in 1999. Bare ground, litter and shrub cover were highest (5.4%, 28.1% and 5.3% respectively) and graminoid and bryophyte cover the lowest (22.5% and 19.3% respectively) in 2008. In 2010, forb and lichen cover were highest (13.3% and 13.3% respectively), while the cover of bare ground and litter was lowest (0.3% and 16.5% respectively). Lichen cover appears to have steadily increased over time (5.2–13.3%), and forb cover shows a similar trend since 1999 (6.5–13.3%).

Change in the relative cover of plant functional groups differed for each plant community (figure 2). The relative cover of bare ground, graminoids, litter and bryophytes in ACG tundra, FG tundra (figure 2 FG) and WG tundra

fluctuated considerably. Shrub cover increased slightly in CAG tundra (CAG, figure 2, 0–3.7%), but showed no change in other plant communities. In PAG tundra, forbs and litter decreased (63.4–26.4% and 32.0–5.5%, respectively), while graminoids increased (4.5–67.8%). In MG tundra forbs and lichen cover increased over time (2.7–9.6% and 9.4–25.9%, respectively) and no change was observed for other functional groups. In DMSG tundra, the cover of forbs and lichens increased (1.3–6.5% and 1.7–27.8%, respectively), while that of graminoids, litter and bryophytes fluctuated. In DSG tundra cover of forbs and lichens increased (10.7–19.5% and 15.9–29.4%, respectively), while the cover of bryophytes (22.6–14.5%) and shrubs (35.1–16.8%) decreased. In SDSG tundra the cover of most functional groups varied between sampling times with the exception of shrubs, which increased slightly (0–2.6%). Repeat photos (figure 3) show a time series of aquatic (CAG tundra), wet-moist (WG tundra), and dry (DSG tundra) community change in 1972, 2000, 2008 and 2010. The most dramatic change in this photo series is for PAG, where there has been a consistent increase in the cover of *Dupontia fisheri* and a reduction in the cover of *Arctophila fulva* over time. There appears to be little obvious change in WG and DSG tundra over time. However, overall plant cover was lowest in 2008, particularly in PAG tundra.

3.3. Change in plant diversity and individual species

Diversity, as measured by both richness and Shannon's index was higher in 2010 than any other sampling date for specific plant communities. In general, plant communities with low soil moisture (e.g. DSG and SDSG) were the most diverse, while communities with higher soil moisture (e.g. ACG, CAG and PAG) were the least diverse. For most plant communities, the greatest increase in richness was between 1999 and 2010, and the largest increase in Shannon index was between 1972 and 2010 (table 1). Between 1972 and 2010, MG, FG and DSG tundra had significant increases in both richness and Shannon index values. For CAG, richness was higher in 2010 than in 1972 but Shannon's index was not, while SDSG and PAG had higher Shannon's index values in 2010 but richness did not differ. Shannon's index values for ACG and WG tundra were significantly lower in 2010 than 1972, but richness did not differ, and the diversity of DSMG tundra showed no long-term difference in either diversity metric.

Of the 19 species that comprised >80% of the overall relative cover (table 2), five had higher relative cover in 2010 than 1972 (*Arctophila fulva, Cetraria islandica, Dupontia fisheri, Luzula arctica* and *Salix pulchra*), and two had lower relative cover (*Salix rotundifolia* and *Saxifraga cernua*). Other changes were detected in the more rare species with long-term increases in *Cardamine pratensis, Saxifraga foliolosa, Stellaria edwardsii, Luzula confusa, Alectoria nigricans, Bryocaulon divergens, Cladonia* spp., and *Thamnolia* spp., and decreases in *Calamagrostis holmii* and *Pseudevernia consocians* (supplementary document 3 available at stacks.iop.org/ERL/7/015508/mmedia). Species changes were generally most significant in plant communities
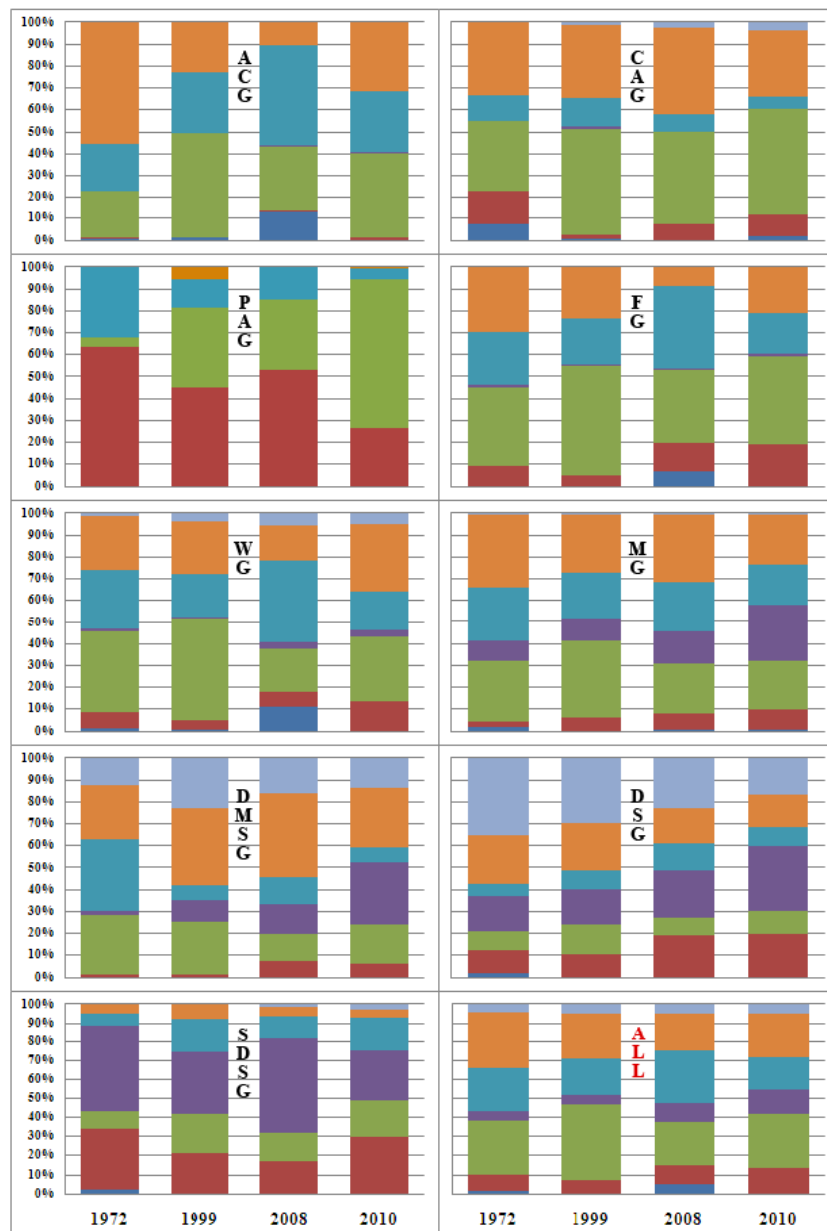
Figure 2. Relative cover of plant functional groups and non-biological categories for each plant community and sampling year (1972, 1999, 2008, 2010) in the coastal tundra near Barrow, Alaska, and for all plots in each sampling year (bare ground—dark blue, forbs—red, graminoids—green, lichen—purple, litter—aqua, bryophytes—orange, and shrubs—light blue).

where they were most common (table 2 and supplementary document 3 available at stacks.iop.org/ERL/7/015508/mmedia).

4. Discussion

Because of the potential impact of climate change on biodiversity and the mobilization of the large stocks of soil organic carbon to the atmosphere (Finzi *et al* 2011), understanding how arctic plant communities have changed over decadal time scales in response to climatic and other change is imperative. While greening of the Arctic has been documented from satellite remote sensing (Bhatt *et al* 2010), and change in ecosystem structure and function has been modeled (Epstein *et al* 2004, Euskirchen *et al* 2009) and appears to have occurred in response to experimental warming (Hudson *et al* 2011) and nutrient addition (Chapin *et al* 1995), relatively few studies have examined change in arctic tundra systems over decadal time scales. Two dominant themes have emerged from this study affirming that plant community change in Barrow is occurring. The first is that short-term community responses to herbivory can be greater than and indeed mask longer-term changes depending on when sites are sampled. The second theme is that no consistent and overarching change is occurring among all plant communities in the Barrow landscape. Instead, most plant communities and functional groups appear to be responding differently over time.
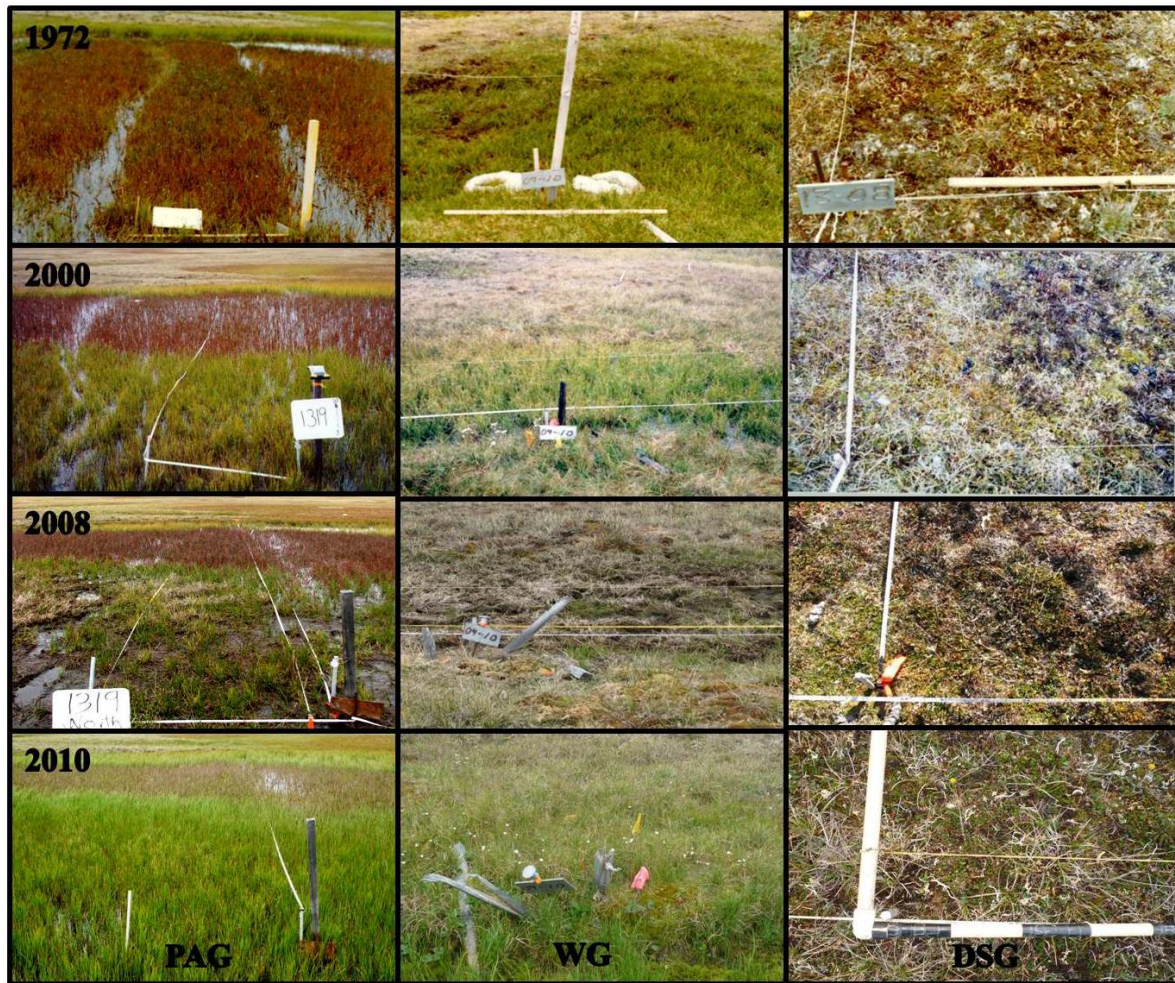
Figure 3. Repeat photographs of three communities from the four sample years (1972, 1999, 2008, 2010) in the coastal tundra near Barrow, Alaska. All photos were taken during peak season. The decrease in biomass in 2008 for all communities occurred during a lemming population outbreak.

4.1. Plant community responses to herbivory mask long-term change

While the interannual variability of species phenology and cover can be substantial for many arctic plant communities (Knorre *et al* 2006), interannual differences in the structure of communities that support large fluctuating populations of lemming such as those near Barrow (Pitelka and Batzli 2007) can be even greater. The large change in vector lengths between 2008 and 2010, relative to other sampling year comparisons, suggests that periodic lemming disturbance can mask long-term vegetation change; the 1972 and 2010 sampling interval had the lowest vector length. Alternatively, periodic lemming herbivory may disturb plant communities resulting in the potential for alternative stable states to develop as has been seen in response to herbivory in other tundra systems (van der Wal 2006). Regardless, the fluctuations in the relative cover of species in communities that are key lemming habitat, such as MG, FG and WG tundra between sampling times are partially explained by lemming herbivory. Lemmings in Barrow typically graze moist plant communities in late summer (Batzli *et al* 1980), which likely explains why

ACG, FG and WG tundra showed low cover of graminoid during the lemming high in 2008. The cover of shrubs and lichens (with the exception of shrubs in DMSG tundra) are not likely to be affected by herbivory directly due to the absence of these functional groups in the diets of lemmings, and also because caribou, which graze on lichens (White and Trudell 1980), are rarely encountered in the study area. However, the overall increase in lichen cover (1972–2010) could be explained by lemming-altered species interactions (Johnson *et al* 2011).

Much of the variability in species cover and plant community change between sampling dates appears to be explained by the time since the last lemming population outbreak, which agrees with the notion that communities respond differently to intense herbivore disturbance (Speed *et al* 2010, Johnson *et al* 2011). Studies have recorded negative impacts on bryophyte abundance primarily as a result of herbivore trampling (Moen *et al* 1993, Virtanen 2000, van der Wal 2006). Our data suggest similar results, with low abundance of bryophytes in 2008 during the lemming high. Outbreaks of lemming populations clearly influence plant community structure in the Barrow area (see also Johnson

Table 2. Mean difference in the relative cover of nineteen species that comprise >80% cover in the sites sampled for all sampling times (1972, 1999, 2008, 2010) in the coastal tundra near Barrow, Alaska. Bold values represent significant differences between 1972 and 2010 ([†] <0.1, [*] <0.05, [**] <0.01, [***] <0.001) from a general linear model assuming a Poisson distribution. Functional groups (FG) include: graminoid (G), evergreen shrub (ES), lichen (L), forb (F) and deciduous shrubs (DS). *Total* describes differences in cover found in all plots.

Species	FG	SDSG	DSG	DMSG	MG	WG	FG	CAG	ACG	PAG	Total
Salix pulchra	DS		**2.8**[†]			**4.2**[***]			0.1		**1.4**[†]
Salix rotundifolia	DS		**−14.0**[***]	−0.8	−0.8	0.9	0.0	**3.3**[*]			**−1.0**[*]
Cassiope tetragona	ES		**−6.5**[***]								−0.6
Petasites frigidus	F	**−6.3**[**]	0.1	0.4	**4.7**[***]	**2.8**[**]	2.9	0.7			1.8
Ranunculus pallasii	F						−0.1	0.6		**−60.3**[***]	−1.8
Saxifraga cernua	F	0.4	−0.3	−1.3	−1.3	**−2.0**[**]	−1.4	−0.2	0.0		**−1.0**[*]
Arctagrostis latifolia	G	**13.7**[***]	**3.0**[**]	1.5	−0.1			**−8.2**[***]			0.3
Arctophila fulva	G							**20.9**[***]		**24.5**[***]	**2.0**[*]
Carex aquatilis	G	1.4	1.2	**−17.3**[***]	**−2.6**[†]	**−6.0**[*]			**34.1**[***]	5.5	2.7
Dupontia fisheri	G	1.6		−1.1	0.9	**−1.7**[†]	4.5	**18.1**[***]	0.3	**23.0**[***]	**2.1**[***]
Eriophorum angustifolium	G	0.3	−1.0	−1.1	−1.4	**−2.2**[*]	**−8.2**[**]	0.3	**1.8**[**]		−1.7
Eriophorum russeolum	G	1.8	0.0		0.2	**−3.0**[***]	**−1.7**[*]	0.6	**3.0**[**]	**6.9**[*]	−0.2
Eriophorum scheuchzeri	G						−0.1				0.0
Hierochloe pauciflora	G								0.1		0.0
Luzula arctica	G		1.3	0.9	**5.2**[***]	0.0	0.5		0.0		**1.2**[**]
Poa arctica	G	−3.4	0.5	−1.8	**−5.2**[***]	1.1	**11.8**[***]		0.2		0.6
Cetraria cucullata	L	1.1	0.9	0.6	**1.1**[**]	0.0					0.3
Cetraria islandica	L	−0.4	**4.1**[*]	**4.3**[*]	**6.0**[***]	**0.6**[*]	0.0		0.0		**1.9**[***]
Dactylina arctica	L	**−4.1**[**]	1.1	**3.5**[**]	**2.2**[*]	0.2	0.1				0.6

et al 2011), highlighting the importance of considering the timing of sampling relative to lemming population cycles, particularly since climate warming is expected to decrease the frequency and amplitude of lemming outbreaks in tundra ecosystems (Ims *et al* 2011).

4.2. Dynamics of plant community change differ between communities

The nine classified plant communities are similar to the eight communities reported by Webber (1978). The additional class is likely a result of both the use of more modern statistical software as well as the division of 43 historic sites, classified by Webber, into 430 individual plots. We feel our analysis correctly identified distinctive plant communities characteristic of the coastal tundra near Barrow. Sustained directional change among all plant communities was not observed. The only exception to this was an overall increase in plant diversity, which contradicts results of passive experimental warming and some observational studies (Walker *et al* 2006), but supports other observational studies (Wilson and Nilsson 2009). The mean annual air temperature near Barrow is increasing, although maritime influences may have lessened the magnitude of warming (Bhatt *et al* 2010, Stone *et al* 2002). However, substantial non-directional movement in ordination space between sampling periods for certain communities, as well as changes in the abundance of species and functional groups, suggests changes are occurring, although the link between climate, hydrology, succession and other change drivers is unclear and a clear cut attribution of change is not possible at this time.

Change was greatest along NMS axis two that correlated with soil moisture, and for the wettest communities, which appear to be the most dynamic over the study period

(1972–2010). ACG tundra demonstrated a linear pattern of change through time, decreased diversity, and increases in graminoid cover (particularly *Carex aquatalis)* to the detriment of bryophytes. Creek *Arctophila* graminoid and PAG tundra also fluctuated through time, but graminoid and overall diversity increased. Flooded graminoid and WG tundra did not fluctuate as much in ordination space, but forbs and graminoids increased. Alternatively, drier communities appear to have changed little over the study period. Moist graminoid, DSMG and DSG tundra all varied little in ordination space, although diversity increased but was largely associated with increases in lichens. In ordination space SDSG tundra also varied little and had lower lichen abundance in 2010 compared to 1972. Combined, these results suggest a slight drying of the overall landscape, which could be related to regional warming, historic draining of nearby lakes in 1950 (Brown 1980) or other factors. Interestingly, Lin *et al* (2012), using multi-temporal classification of aerial and satellite imagery, suggest that a tundra landscape several kilometers from the study, and not affected by anthropogenic drainage, has generally dried over the past 60 years. In his study, the extent of dry and moist tundra increased and that of wet tundra decreased over time, which agrees with findings in this study. Our results for changes in shrub cover are somewhat consistent with other long-term observations and experimental studies that report increased shrub abundance (Myers-Smith *et al* 2012, Tape *et al* 2006, Walker *et al* 2006, Sturm *et al* 2001). These studies have shown increases in erect dwarf shrubs similar to what we report for the erect deciduous shrub *Salix pulchra*. However, in this study, we documented decreases in the cover of the prostrate evergreen shrub *Cassiope tetragona* and deciduous shrub *Salix rotundifolia*. Overall, we believe that the decreased cover of *C. tetragona*

and *S. rotundifolia* cancelled out the increase in *S. pulchra*, which resulted in no change in shrub cover when analyzed as a functional group. This highlights the importance of detecting individual species responses to warming, which can otherwise be masked when species are lumped in functional groups.

Communities dominated by bryophytes and sedges (ACG, CAG, PAG, FG, MG) show an increase in lichens and shrubs between 1972 and 2010 (with the exception of MG tundra) whereas communities dominated by bryophytes, sedges, and shrubs (DMSG, DSG) show increases in lichens and forbs and not shrubs. These results agree with warming simulation trends described by Epstein *et al* (2000, 2004) that report increases in lichens in both high and low arctic ecosystems after 50 years. Shrubs increased in DSG tundra but not in SDSG tundra, likely due to the different change responses in the different shrub species described above.

5. Conclusion

Resampling of plant communities in historic research plots suggests that change in plant communities, functional groups, and species can be dynamic and different for different plant communities. The short-term response of vegetation to lemming population outbreaks can mask long-term change. Graminoids and bryophytes decrease in abundance during outbreak years while litter and bare ground increase. Over the 38-year study period, diversity increased for most plant communities, and wetter communities changed more than dry and moist plant communities. A slight drying trend appears to be occurring at the study site but the climatic factors and hydrologic processes related to this are unclear. The continued effort to conclusively understand how tundra landscapes are responding to warming is important considering the potential consequences of feedbacks from these landscapes to the global system and the variability and complexity associated with temporal change dynamics in arctic tundra systems.

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