Post-fire herbivore impacts

Small herbivores with big impacts: tundra voles (*Microtus oeconomus*) alter post-fire ecosystem dynamics

Authors: Jess K. Steketee*[,1], Adrian V. Rocha[2], Laura Gough[3], Kevin L. Griffin[4,5,6], Ian Klupar[2], Ruby An[7], Nicole Williamson[3], Rebecca J. Rowe[1]

[1]Natural Resources and the Environment, University of New Hampshire, 114 James Hall, 56 College Road, Durham, NH 03824 USA

[2]Department of Biological Sciences and the Environmental Change Initiative, University of Notre Dame, Notre Dame, IN 46556 USA

[3]Department of Biological Sciences, Towson University, Towson, Maryland 21252 USA

[4]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA

[5]Department of Earth and Environmental Sciences, Columbia University, Palisades, NY 10964, USA

[6]Lamont-Doherty Earth Observatory, Columbia University, Palisades NY 10964, USA

[7]Department of Ecology and Evolutionary Biology, Princeton University, Princeton NJ 08540

*Email: jksteketee@wildcats.unh.edu

Open Research Statement: Data supporting this research is not yet provided. Should this paper be accepted, data will be permanently archived in the Dryad Digital Repository prior to publication.

Abstract: Fire is an important ecological disturbance that can reset ecosystems and initiate changes in plant community composition, ecosystem biogeochemistry, and primary productivity. Since herbivores rely on primary producers for food, changes in vegetation may alter plant-herbivore interactions with important – but often unexplored – feedbacks to ecosystems. Here we examined the impact of post-fire changes in plant community composition and structure on habitat suitability and rodent herbivore activity in response to a large, severe, and unprecedented fire in northern Alaskan tundra. In moist acidic tundra where the fire occurred, tundra voles (*Microtus oeconomus*) are the dominant herbivore and rely on the tussock forming sedge *Eriophorum vaginatum* for both food and nesting material. Seven to twelve years after the fire, tundra voles were 10 times more abundant at the burned site compared to nearby unburned tundra. Fire increased habitat suitability for voles by increasing plant productivity and biomass, food quality, and cover through both taller vegetation and increased microtopography. As a result of elevated vole abundance, *Eriophorum* mortality caused by vole herbivory was two orders of magnitude higher than natural mortality and approached the magnitude of the mortality rate resulting directly from the fire. These findings suggest that post-fire increases in herbivore pressure on *Eriophorum* could, in turn, disrupt graminoid recovery and enhance shrub encroachment . Tundra state transitions from graminoid to shrub dominated are also evident following other disturbances and fertilization experiments, suggesting that as Arctic temperatures rise, greater available nutrients and increased frequencies of large-scale disturbances may also alter plant-animal interactions with cascading impacts on plant communities and ecosystem function.

Keywords: Arctic, herbivory, plant-animal interactions, rodent, moist acidic tussock tundra, *Eriophorum vaginatum,* disturbance, Anaktuvuk River fire, succession

Introduction

Plant-animal interactions have substantial impacts on ecosystem processes yet are rarely included in projections of ecosystem function associated with climate change. These interactions may be disrupted under environmental change and intensifying disturbance regimes (Post et al. 2009), with unknown consequences on carbon cycling. Wildfire is a natural disturbance that is increasing under warming (Young et al. 2017, Jones et al. 2020), with great potential to modify both antagonistic (e.g., Wan et al. 2014, García et al. 2016) and mutualistic (e.g., Lybbert and St. Clair 2017) plant-animal interactions. Here we investigate the impacts of a decade of post-fire successional change on habitat suitability for rodent herbivores and potential feedback effects of altered herbivore pressure on ecosystem function in arctic tundra. Following fire, the tundra undergoes large changes in plant community composition, canopy structure, net primary productivity, and nutrient cycling (Rocha & Shaver 2011, Bret-Harte et al. 2013, Klupar et al. 2021). These changes impact the quality and availability of resources (food and habitat) for wildlife (Joly et al. 2007), which can lead to marked changes in distribution and density, and thus herbivore pressure. Selective herbivory can shape plant composition and productivity, with cascading impacts on decomposition rates and carbon and nutrient cycling (Huntly 1991, Gough et al. 2007, Post et al. 2009, Ylänne et al. 2015). The consequences of successional changes for wildlife and plant-animal interactions are poorly understood, especially in ecosystems where fire is rare.

Disturbance and herbivory often work in concert to regulate plant community composition, either promoting recovery along a successional pathway to a pre-disturbance state or transitioning the ecosystem to an alternative state. Transition states are common in grassland and savannah ecosystems where fire is a natural disturbance. For example, in North American grasslands, greater browsing pressure along with frequent fire can limit woody encroachment and maintain grassland conditions (O'Connor et al. 2020, Collins et al. 2021), while post-fire grazing by non-native species transitioned Argentinian forest to shrubland (Raffaele et al. 2011) and, in African savannas, the systems transitions from grassland to shrubland depending on the fire frequency and level of grazing and browsing (e.g., Van Langevelde et al. 2003). Similarly, outbreaks of herbivorous insects can trigger ecosystem state transitions, both as independent disturbance agents and in association with fire or ungulate herbivory (McCullough et al. 1998, Vindstad et al. 2019). For example, in Scandinavia, increasingly severe outbreaks of geometrid moths may change birch understory to graminoid tundra (e.g., Karlsen et al. 2013) and additive effects of reindeer herbivore pressure can further prevent boreal forest regeneration (Lehtonen and Heikkinen 1995, Biuw et al. 2014). Rates and patterns of vegetation change, including the likelihood of ecosystem state-transitions, are often context dependent and can be difficult to predict, especially in places undergoing shifts in disturbance regimes.

Although historically rare, tundra wildfires are increasing in frequency and severity due to climate change (Kasischke & Turetsky 2006; Rocha et al. 2012; Hu et al. 2015), and are most common in moist acidic tussock tundra (MAT) (Rocha et al. 2012). MAT is characterized by the common sedge species *Eriophorum vaginatum*, that forms dense root mounds called tussocks. Although *Eriophorum* is one of the first plants to recover after fire (Wein and Bliss 1973, Racine et al. 1987), successional pathways can be diverse, either returning to pre-fire graminoid dominated communities, or shifting to shrub dominated (Racine et al. 2004, Barrett et al. 2012, Jones et al. 2013, Chen et al. 2020, Frost et al. 2020, Klupar et al. 2021). These changes in plant community composition and structure can have cascading impacts on resource availability and habitat suitability for wildlife.

Post-fire successional impacts on habitat suitability disproportionally affect herbivores that rely on plants for both shelter and food resources. The tundra (or root) vole (*Microtus oeconomus*) is the most abundant herbivore in tussock tundra. Like most rodents, tundra vole population dynamics and space use are closely tied to resource availability and quality (Batzli and Lesieutre 1991, Forbes et al. 2014). Tundra voles rely on *Eriophorum* as a staple in their summer (tillers) and winter (rhizomes) diet (Batzli and Henttonen 1990) and use the tillers and tussock structures to create winter nests.

Post-fire soils tend to have higher nutrient availability due to increased nutrient mineralization (Jiang et al. 2015), which can increase plant productivity and nutrient concentrations. Herbivores are nutrient (i.e., nitrogen) limited (Mattson 1980), and both natural and manipulative experiments show increases in available food (in particular protein content) directly result in higher rodent densities (Tast 1972, Cole and Batzli 1979, Batzli and Lesieutre 1995, Forbes et al. 2014). Tundra fires can also alter habitat suitability via structural changes in the canopy or surface topography. Increases in canopy height can increase snow depths by acting as windbreaks (Sturm et al. 2000) and thus facilitate a warmer, less variable subnivean layer that is critical for rodent winter survival (Korslund and Steen 2006, Duchesne et al. 2011, Reid et al. 2012, Pauli et al. 2013). Increased micro-topography results from the removal of the soil organic and moss layers (Mack et al. 2011, Abbott et al. 2021), the persistence of *Eriophorum* tussocks, and subsidence of the surface due to greater post-fire permafrost thaw (Jones et al. 2015).

Post-fire changes in food quantity, quality and available cover may alter rodent population density and herbivore pressure, with cascading impacts on plant productivity and community composition. Rodent impacts result from selective foraging, clipping green leaves, concentrating nutrients through fecal latrines, and establishing nests and runways. During years with large vole populations, extensive clipping and tunneling can damage slow-growing plants to the benefit of fast-growing species (Dahlgren et al. 2009, Tuomi et al. 2019). These effects are species specific, and tundra voles, unlike many other microtine species, are not known to girdle shrubs. Selective foraging by voles has also been shown to hasten the transition from graminoid to shrub dominance in fertilized tundra experiments (Gough et al. 2012), but the importance of herbivory on post-fire impacts are currently unknown.

Here, we examined wildfire impacts and interactions between tundra voles and their post-fire habitat a decade after the 2007 Anaktuvuk River fire, the largest recorded tundra fire on the North Slope of Alaska. We hypothesize that post-fire vegetation will improve habitat for tundra voles, which will increase population density and thus herbivore pressure, which will negatively impact the biomass of their preferred resource over the longer term. Understanding how fire impacts resources for the most abundant herbivore and subsequently herbivore pressure, is important for predicting post-fire impacts on successional dynamics and ecosystem function, especially as disturbance regimes shift in a rapidly warming Arctic.

Methods

Site Description and Study Design

This study was conducted at a severely burned site and an unburned (control) site within the southern portion of the 2007 Anaktuvuk River fire scar (Rocha and Shaver 2009, 2011a). The Anaktuvuk River fire, an unprecedented event in the past 5000 years, burned 1000 km^2 of moist acidic tussock (MAT) tundra (Jones et al. 2009). The sites (ca. 2500m^2 areas within the fetch of meteorological towers) were established a year after the fire and are 7 km away from each other, with similar pre-fire homogeneous MAT vegetation, soil, topography, and weather conditions (Rocha and Shaver 2011b). The burned site experienced 100% loss of vegetation cover (Jones et al. 2009) and a 30% loss in the soil organic horizon (Mack et al. 2011). *Eriophorum* tussocks recovered quickly as a result of their high bulk density and moisture content, which reduced their flammability. These mounds protected *Eriophorum* rhizomes that allowed for resprouting and rapid growth of tussocks during the first post-fire growing season. Other vascular plants (forbs and graminoids) also recovered within 4-5 years after the fire (Bret-Harte et al. 2013) and shrubs are beginning to dominate the landscape (Klupar et al. 2021) but the soil organic horizon has not yet recovered (Abbott et al. 2021). The unburned site was unaffected by the fire and the vegetation typical of MAT, dominated by graminoids (in particular *Eriophorum vaginatum*), evergreen and deciduous shrubs, mosses, and lichens (Appendix S1: Table S1). Our study, like other "natural experiments", consists of a single treatment (burned) and control (unburned) site and thus our replicates are not independent. To place our observations in the broader context and to better infer causality, we draw on previous observational and experimental studies conducted in MAT.

Productivity and Plant Biomass

Each site was equipped with a meteorological tower that measured environmental variables every half hour during the 2008-2019 growing seasons (May-September). Instrumentation specifications are described in detail in Rocha and Shaver (2009) and Rocha and Shaver (2011). Average daily surface greenness (i.e., the 2 band Enhanced Vegetation Index [EVI2]) was calculated using average daily incoming and outgoing solar and photosynthetically active radiation as described in Rocha and Shaver (2009) and Rocha et al. (2021).

Vegetation biomass measurements were taken during an aboveground biomass harvest at peak growing season (late July) in 2017. Vegetation was sampled randomly at 10-m intervals along two 100 meter transects situated east and west of the meteorological tower at both the burned and unburned site. Vegetation was sampled within a 10X40 cm quadrat to the mineral layer with a bread knife. Samples were placed in plastic bags and transported to the lab for processing where the plant material was sorted into new and old aboveground leaf and woody biomass by species. All samples were dried at 60ºC for 3-4 days and weighed. We scanned subsampled leaf material to determine specific leaf area (cm^2 g^{-1} biomass) per species, which was then used to transform leaf biomass (g m^{-2}) into the leaf area index (LAI) for each site. New aboveground biomass (i.e. biomass grown in current year) was summed and used to determine Aboveground Net Primary Productivity (ANPP; g m^{-2} y^{-1}) for each site. Plant species were grouped into growth forms according to structural tissue and leaf phenology: deciduous shrubs, evergreen shrubs, graminoid/sedge, forbs, moss, and lichen (Appendix S1: Table S1).

Canopy Height

Canopy height was determined using the point intercept method with five replicates per site. A 0.56 m^2 frame with 41 evenly spaced sampling points was placed at a leveled height above the canopy at each site during the peak of the 2019 growing season. From each of the 41 sampling points, a 1 m long and 3 mm wide pin was dropped vertically, and the height and species of the tallest vegetation-pin contact was recorded to the nearest cm. Therefore, species height is the average of the tallest individuals within a frame. Species were grouped by growth form (Appendix S1: Table S1).

Microtopography

Tussock height and diameter were measured to characterize differences in microtopography at the two sites. Greater terrain ruggedness might decrease mobility and thus hunting success of terrestrial predators (e.g., foxes and weasels) while also providing greater protection which might decrease detection by avian predators (e.g., Jaegers). Tussock height measurements were taken in 2016 along four 100 meter transects located in each cardinal direction from the meteorological tower. For each tussock intercepted by the transect tape, we measured the diameter in two directions (N-S & E-W) with a caliper, and the distance between the soil surface to tussock top in the four cardinal directions with a ruler.

Tussock Nitrogen Content

To examine the quality of plants as forage for rodents, we measured percent nitrogen in *Eriophorum* rhizomes and tillers. For rhizomes, this was calculated from pooled samples taken in late July 2018 at the burned and unburned sites during an aboveground biomass harvest. Sampling consisted of 5 blocks (4mX5m) per site, with two plots (10X40cm) sampled per block, for a total of 10 plots per site. *Eriophorum* rhizomes were present in 6 plots at the burned site and 8 plots at the unburned site. Rhizomes were dried at 60˚C for 24 hours, ground and homogenized, with equal rhizome weights from each plot pooled and analyzed for elemental composition (%N) at the University of New Hampshire Stable Isotope Laboratory using an Elementar Americas

Pyrocube elemental analyzer. Rhizome percent nitrogen was scaled up to rhizome nitrogen m^{-2} using rhizome biomass values obtained from aboveground biomass pluck (described above).

Tillers were collected for nitrogen analysis in late July 2019. Twenty-four tussocks in total were sampled, within a 30m radius of the meteorological tower, from burned and unburned sites. At the burned site, 8 tussocks with evidence of vole herbivory (i.e. damage to rhizomes) and 8 tussocks without herbivory were sampled; at the unburned site, 8 tussocks without herbivory were sampled. At the burned site, tussocks with and without herbivory were sampled to separate herbivore effects from those of the fire. From each tussock, 3-4 new leaves were sampled (as indicated by lack of brown tips) and dried at 60° C for 24 hours. Leaves were ground and analyzed for nitrogen (%N) composition with an Elementar Vario EL III CHNOS Elemental Analyzer at Towson University.

Tussock Density, Mortality, and Herbivore Activity

Tussock density, mortality, and herbivore activity were determined during the summer 2019 growing season. At each site, three 50 meter transects were set in the North, West, and East side of the meteorological tower. All tussocks were counted and classified into living, dead, and vole-grazed categories every 1 meter along each transect within a 1 m^2 quadrat. Living tussocks were identified by their green leaves and flowering tillers. Dead tussocks were identified as tussocks that lacked leaves and flowers and were further classified by cause of death (i.e. fire, grazed, and natural). Tussocks that died by fire were dark or greyish in color (clearly charred) and lacked evidence of post-fire green leaves, litter, and flowers. Tussocks that died by herbivory had evidence of post-fire leaf growth and litter accumulation, but had rhizomes and tillers that were completely eaten off the top of the tussock. Tussocks that died from natural causes were distinguished as those with litter accumulation that lacked evidence of herbivory, green leaves, and flowers. We also classified the severity of grazing on each of the living tussocks into severe, major, and moderate herbivory categories. Severe herbivory was defined by 100% herbivory of *Eriophorum* rhizomes and vegetation and resulted in mortality. Major herbivory was defined as consumption of both rhizomes and tillers, while moderate herbivory was defined as consumption of tillers only. Vole litter piles, nests, fresh latrines, and well-trodden burrows and runways were counted in each of the 1 m^2 quadrats as another measure of herbivore activity.

To quantify biomass loss due to vole herbivory, we harvested twenty grazed and seven ungrazed tussocks in late June 2019 from the burned site. In the field, we took two measurements of tussock diameter along the major north-south and east-west cardinal directions with calipers. These tussocks were marked and transported to the lab for separation into litter, rhizomes, and green leaf biomass pools. The plant material was then dried at 60°C for two days and weighed. Carbon (C) content of biomass were determined with a Costech elemental analyzer calibrated with NIST peach leaves standard at the University of Notre Dame. For the ungrazed tussocks, we developed allometric relationships between diameter and biomass for each of the three pools using non-linear least squares regression (R^2=0.86; Curasi et al. In Review). This allometry was used to predict expected biomass in the grazed tussocks, where the difference between predicted and measured biomass quantified the lost biomass due to herbivory for each of the grazed tussocks. The average biomass lost from herbivory from all tussocks was then scaled up to 1 m^2 using the grazed tussock density at the burned site. These upscaled estimates reflect the cumulative herbivore impacts over the decade since the fire. For reference, we compare these herbivore impacts to the annual forage biomass and productivity measurements taken in 2017.

These estimates were conservative since sampling only included grazed tussocks with active leaves and tillers.

Herbivore Abundance

Small mammals (rodents and shrews) were trapped at the burned and unburned sites in August of 2014 and 2017-2019. At each site, three parallel 400-meter trap lines separated by ca. 40 meters were set with traps stationed every 10 meters. One Museum Special snap-trap was baited with peanut butter and oats and set to sign (e.g., runway or latrine) within a meter of the trap station. Traps were set during the afternoon and checked/reset the following two mornings for a total survey effort of 240 trap nights (one trap, set one night). Abundance estimates were corrected for sprung traps (Beauvais and Buskirk 1999). Captures were pooled according to site and year, and a capture index was calculated per 100 trap nights. A paired t-test was used to compare tundra vole captures between sites and years. All captures were identified to species. Voucher specimens were deposited at the University of Alaska Museum. Survey procedures followed the guidelines of the American Society of Mammalogists (Sikes et al. 2016) and were certified by the UNH Animal Care and Use Committee (protocols 140308, 161005).

Welch two-sample t-tests were used to compare vegetation measurements between the burned and unburned site, and when normality assumptions could not be satisfied, a Wilcoxon test was used instead to compare nitrogen content, tussock diameter, biomass of grazed and ungrazed tussocks, LAI, canopy height and rodent activity. Response variable distributions were assessed for normality using Shapiro-Wilk test, and visually assessed for normality, skewness and outliers using histograms, density plots and boxplots. All statistical analyses were performed with the program R (RStudio Team 2019), with a cutoff of $p < .05$ for inferring statistical significance.

Results

Landscape-scale changes in productivity & plant community structure

As reported in Klupar et al. (2021) and Abbott et al. (2021), post-fire successional changes in vegetation increased overall landscape productivity. In the first four years, EVI2, an index of vegetation greenness, was lower at the burned compared to the unburned site. After five years (2012), EVI2 reached and exceeded pre-disturbance levels as documented at the unburned site, before returning to pre-disturbance levels in years 2016-2019 (Fig. 1). This indicates post-fire succession may temporarily yield higher productivity than undisturbed MAT. Biomass derived LAI indicates the elevated productivity at the burned site is due to greater graminoid and forb biomass (graminoid; 1.04+/-0.24 SE compared to 0.33+/-0.73 $p < 0.02$, forb; 0.59+/- 0.17 compared to 0.19+/- 0.06 $p = 0.008$, Fig. 2a) with a non-significant trend of greater deciduous shrub LAI (0.68+/-0.19 compared to 0.27+/-0.09 $p = 0.26$, Fig. 2a). Total canopy height was also significantly taller at the burned site by an average of 13.5 cm ($W=25$, $p = 0.01$), and with the exception of forbs, all growth forms were taller (Fig. 2b). The greatest difference in height was in deciduous shrubs, which were on average 20 cm (39.6 +/-1.87 compared to 19.6+/-3.69) taller at the burned site.

Changes in rodent habitat suitability: food quality, quantity, & vegetation structure

Eriophorum tussocks provide critical food and nesting resources for tundra voles and contribute to overall habitat structure. Although tussock density was lower at the burned site, tussocks were larger and *Eriophorum* more abundant (Table 1, Fig. 2a; Klupar et al. 2021). Average tussock mound diameters were larger by 4 cm (Table 1, $p < 0.001$), and average mound heights (excluding tillers) taller by 9 cm (Fig. 3a, b, $t_{146.63} = 10.56$, $p < 0.001$).

Differences in forage quality were also evident. Tussock rhizomes (winter forage for voles) had greater %N at the burned compared to the unburned site (Fig. 3c). Although tussocks were less dense at the burned site, the combination of larger tussocks and greater nitrogen content compensated for the decrease in density (1.3gN tussock^{-1} compared to 0.3gN tussock^{-1}, $p < 0.001$). When total N in rhizomes was determined at the plot level (1 m^2), total rhizome N (gN rhizomes m^2) was 3 times greater at the burned site as compared to the unburned site (1.25 +/- 0.41 compared to 0.32+/- 11 gNm^2, $p < 0.001$, Fig. 3c). No difference in tiller (summer forage) % N was detected between sites, or between grazed and ungrazed tussocks; average values for both burned and unburned sites was 1.87%.

Impacts on rodent density

In each of the four years surveyed, tundra voles were more abundant at the burned site with an average of 5.4+/-1.34 compared to 0.5+/-0.26 individuals per 100 trap nights (Fig. 4a, Appendix S1: Fig. S1, $p = 0.02$). While it is not clear whether tundra vole populations in this region regularly cycle, our data do support that they undergo dramatic fluctuations in abundance, with a 130% difference between high and low capture rates at the burn site, and 200% at the unburned site. Insectivorous shrews followed a similar pattern, while red-backed voles (*Myodes rutilus*) were only detected in two years at the unburned site only (Appendix S1: Fig. S1). Density of rodent activities in 2019 (e.g. fresh runways, winter nests, burrows) was two orders of magnitude greater at the burned site, with 2+/-0.13 activities recorded m^{-2} compared to 0.01+/-0.01 m^{-2} at the unburned site ($p < 0.001$, Fig. 4b). These activities were largely reflective of current summer and previous winter activities; winter nests are ephemeral and while some rodent sign may persist over multiple years, we looked for fresh latrines, green clippings and well-trodden burrows and runways.

Rodent herbivore impacts on Eriophorum biomass

Overall, tussock mortality from vole herbivory was two orders of magnitude higher than natural mortality (5% vs 0.05%) and is closer in magnitude to the mortality rate resulting from the fire disturbance event (21%; Fig. 5a). Additionally, 41% (+/- 2%) of live tussocks at the burned site showed tiller and/or rhizome damage from voles compared with zero at the unburned site. Intensity of herbivory also varied among these live tussocks (n=524), with 17% exhibiting moderate levels, 17% major, and 7% severe. Tussocks that were grazed had significantly less biomass than those without evidence of vole herbivory (220g +/- 27.5 compared with 341+/- 22.8; $p < 0.002$, Fig. 5b). Tissue comparisons indicate the decrease in biomass results from significant difference in both rhizome (17.3+/- 3.6 compared to 66.5 +/-7.8) and tiller (9.8 +/- 2.1 compared to 31.9 +/- 5.1) biomass ($p > 0.001$, Fig. 5b). Although litter (including standing dead) also displayed this pattern (192.7 +/- 24 compared to 242.5 +/- 22.8), the differences were not significant ($p < 0.09$, Fig. 5b). In the decade since the fire, voles removed an average of 70g biomass per tussock (or 35 gC tussock^{-1}, and 120 gC m^{2} +/-14.6). Although herbivory likely occurred over many years, it's cumulative impact in 2019 was comparable to almost a year's worth of total plant productivity (68% of ANPP)) and a substantial amount of total available tussock biomass (20%) at the burned site.

Discussion

Post-fire landscapes dramatically increased tundra vole populations. Previous studies of arctic animals have shown variable responses to fire mediated by changes in resource availability. Tundra songbirds are resilient to short-term fire driven habitat changes (Pérez et al. 2018), while many arthropods respond favorably to burn scars (A. Koltz pers. comm.). However, caribou, which rely on slow-growing lichen species for winter forage, show long-term negative responses and avoid grazing in burned tundra, an effect still evident 55 years after the fire (Joly et al. 2007). Our results demonstrate that mid-successional changes in vegetation post-fire enhance habitat suitability for tundra voles through a combination of increases in food quality, quantity and cover. The increase in vole population size and herbivore pressure, in turn, increased tussock mortality by two-orders of magnitude over natural mortality. Tussock mortality, due to the combined effects of fire and fire driven increases in herbivory, may ultimately shift the post-fire trajectory away from the pre-fire graminoid dominated community, to one that is shrub dominated.

Changes in rodent habitat suitability: food quality, quantity, & vegetation structure

Tussock tundra at the burned site provided greater resources for tundra voles, as measured through productivity and plant biomass (food quantity), nitrogen content (food quality), and vegetation structure (cover), all factors known to impact vole densities (Krebs 2013). In North American arctic systems, herbivorous rodents are not typically limited by food quantity (Krebs 2013, Bilodeau et al. 2014). Although rodents exhibit dramatic yet regular inter-annual fluctuations in density and have significant impacts on plant biomass at peak densities, forage remains abundant during cyclic population declines (Krebs 2013). Therefore, changes to food quality, rather than quantity, are more likely to have contributed to the increase in rodent density at the burned relative to unburned site.

Food quality is influenced by changes in plant composition (increased occurrence or abundance of more palatable species) as well as changes in nutritional quality of species. Tundra voles selectively forage on graminoids, which have been shown to be of high quality, supporting greater growth (Batzli and Lesieutre 1991), and their distribution across different tundra plant communities corresponds to the availability of preferred food items (Batzli and Henttonen 1990). Although both sites are MAT and thus rich in graminoids, *Eriophorum vaginatum, Carex bigelowii,* and *Calamagrostis canadensis* (a typical post-fire invader, Wein & Bliss 1973; Racine et al. 2004) were greater in biomass at the burned site. Following an Alaskan boreal forest fire, tundra voles colonized early successional habitat after *Calamagrostis canadensis* became abundant (West 1979, 1982), suggesting the post-fire increase in tundra voles likely coincided with graminoid recovery. Nitrogen content was higher among *Eriophorum* tussock rhizomes (but not tillers) at the burned site compared to the unburned site, indicating that fire facilitated higher quality winter forage for voles, which could enable greater reproductive output in early spring. These results are consistent with studies on tussock nutrient allocation under fertilized conditions – excess nutrients are stored in overwintering rhizome structures and redistributed in spring to support greater tiller growth (but not greater tiller nutrient concentrations) (Shaver et al. 1986). Fertilization experiments also demonstrate that higher-quality food increases vole abundance and winter activity (Grellmann 2002, Treberg et al. 2010, Gough et al. 2012). Food experiments further provide a direct link between high-quality food (in particular high nitrogen content) and elevated vole densities (Batzli and Lesieutre 1995) through greater survival, reproduction, and smaller home ranges that facilitate immigration (e.g., Cole & Batzli 1979; Taitt et al. 1981; Desy & Thompson 1983; Forbes et al. 2014).

Experimental studies also suggest that greater cover is just as effective at increasing vole densities as high-quality food addition treatments (Taitt et al. 1981). Cover reflects the functional role of vegetative structure, combining elements of reduced predation and/or perceived risk, as well as increased protection from the elements (Birney et al. 1976, Krebs 2013). Both reduced predator pressure and reduced perception of risk have been shown to result in greater reproductive rates and vole densities (Ekerholm et al. 2004, Dahlgren et al. 2009, Dehn et al. 2017). We found taller vegetation in all functional groups except forbs, with the greatest difference in deciduous shrubs, which is consistent with other post-fire studies (Racine et al. 2004; Heim et al. 2021). The increase in tussock height may be due to a combination of factors, including greater productivity, combustion of the organic layer and lack of moss regrowth, and surface subsidence (which doubled following the fire; Jones et al. 2015).Despite decreased tussock density in response to the fire, increased tussock height and biomass could serve to reduce avian and canid predation through inhibited mobility and sight.

Greater vegetation height and surface roughness also provide substantial benefits to rodent populations during snow covered months when subnivean quality is critical for survival (Pauli et al. 2013). Voles remain active underneath the snow and rely on the subnivean layer to provide a stable, insulated environment from which to access food (i.e. tussock rhizomes). Greater vegetation height can increase snow accumulation (Sturm et al. 2000, Myers-Smith and Hik 2013), which generally improves overwintering conditions through increased access to food and more stable temperatures in the subnivean (Korslund and Steen 2006, Berteaux et al. 2017). Deep snow also buffers against variable winter weather (freezing rain or freeze/melt cycles), which can reduce overwinter survival (Aars and Ims 2002, Korslund and Steen 2006). Another arctic rodent (brown lemming) preferentially placed nesting sites in areas with greater microtopography, steeper slopes (Duchesne et al. 2011) and greater snow cover (Reid et al. 2012, Bilodeau et al. 2013). As winters become more stochastic, protected microhabitats may be increasingly important to overwinter survival and population dynamics (Pauli et al. 2013, Berteaux et al. 2017).

Rodent herbivore impacts on vegetation

We found vole densities to be on average 10 times higher at the burned site, with the cumulative (multi-year to decadal) impacts of vole herbivory approaching annual net primary production (120 gC m^2 vs. 180 gC m^2), with an estimated 20% of total forage biomass removed. In Scandinavia, herbivore-driven decreases in local plant biomass have reached similar levels (12-24%) in just one year after rodent (vole and lemming) populations were at their peak (Olofsson et al. 2012). Fertilization experiments suggest removal of plant material by rodents can reach up to 80% in nutrient amended plots following very high densities of overwintering voles (Grellmann 2002). Vole herbivory had a disproportionate impact on their primary resource through removal of tillers and rhizomes, resulting in increased mortality (5% compared to .05%) of *Eriophorum.* Voles targeted nutrient rich rhizome and tiller bases, making it unlikely that damaged tussocks will recover. Because *Eriophorum* germination rates are low (McGraw and Shaver 1982), these increases in mortality will have long-lasting impacts on the post-fire success of *Eriophorum*. Herbivores impact plant community composition through selective foraging which can facilitate competitive release of non-preferred species, (Huntly 1991, Ravolainen et al. 2014, Christie et al. 2015). Fertilization experiments demonstrate that under elevated nutrient conditions, dwarf birch (*Betula nana*) becomes more dominant in moist acidic tussock tundra (Gough et al. 2012; Gough & Johnson 2018; Klupar et al. 2021). Our study suggests that selective foraging by tundra voles may play a secondary role, further decreasing graminoid abundance. Tussocks have less tolerance to herbivory under enriched soil nutrients; grazed tussocks are disadvantaged by both loss of nutrients from rhizome damage and light limitation from damaged tillers and competitive growth of overtopping, non-palatable shrubs (Gough et al. 2012, Johnson and Gough 2013).

Implications for future vegetation change and ecosystem function

Fire generated trajectories often show patterns of increased productivity followed by shifts from graminoid to shrub-dominated communities (Racine et al. 2004, Narita et al. 2015, Heim et al. 2021). Similar system state transitions have been observed at a 30-year-old thermokarst site (Schuur et al. 2007), permafrost degraded "slump" sites (Lantz, 2009), and under fertilization experiments (Shaver and Chapin III 1995, Shaver et al. 2001, Sistla et al. 2013, Klupar et al. 2021). Each of these disturbance types results in an increase in soil nitrogen, which facilitates arctic shrub encroachment.. Warming is expected to increase both available nitrogen and the scope and severity of environmental disturbances (Jorgenson et al. 2006, Lantz et al. 2009, Rocha et al. 2012, Hu et al. 2015). Degraded permafrost and an increase in shrubs may, in turn, translate to greater fuel loads and thus perpetuate increases in the severity and extent of tundra fires (Hu et al. 2015, McCarty et al. 2021). Thus, changes in climate and disturbance regimes are likely to further shift the tundra ecosystem state from graminoid to shrub-dominated. Our finding of increased rates of herbivory (41%) and mortality (5% vs. 0.05%) of tussocks at the burned site raise concerns about the resiliency of MAT to a change in fire regime, and illustrate how fire-driven changes in herbivore pressure may exacerbate this transition from graminoid to shrub-dominated tundra. However, much is unknown regarding fine-scale and long-term trajectories of post-fire plant communities in the Arctic and, in turn, how future rodent densities, distributions, and plant-animal interactions will be altered (Ims and Fuglei 2005, Gilg et al. 2009). Additional multi-trophic studies are needed to better understand response to disturbance. In addition, models predicting future consequences of warming should incorporate the feedback effects of animals in these systems.

Acknowledgments

We thank Alexis Blanchard, Earl Johnson, Laura Knutsen, Cody Lane, Rebecca Levine, Andrew Maguire, Margaret Oliver, Ryan Stephens and Bryce Woodruff for assistance with small mammal surveys, Heather Buelow, Lilly Conteh, Salvatore Curasi, Abbey McCarthy and Felix Yepa for tussock measurements and collection, and the many people who assisted in the field and in the lab on the biomass plucks. We thank the ARC LTER, Toolik Field Station, and CH2MHill Polar Services for logistical support. Funding was provided by the National Science Foundation (1637459 to ARC LTER, 1603760 to LG, 1556772 to AVR, and 1603654 to RJR).

Literature Cited

Aars, J., and R. A. Ims. 2002. Intrinsic and Climatic Determinants of Population Demography: The Winter Dynamics of Tundra Voles. Ecology 83:3449–3456.

Abbott, B. W., A. V. Rocha, A. Shogren, J. P. Zarnetske, F. Iannucci, W. B. Bowden, S. P. Bratsman, L. Patch, R. Watts, R. Fulweber, R. J. Frei, A. M. Huebner, S. M. Ludwig, G. T. Carling, and J. A. O'Donnell. 2021. Tundra wildfire triggers sustained lateral nutrient loss in Alaskan Arctic. Global Change Biology:408–1430.

Barrett, K., A. V. Rocha, M. J. Van De Weg, and G. R. Shaver. 2012. Vegetation shifts observed in arctic tundra 17 years after fire. Remote Sensing Letters 3:729–736.

Batzli, G. O., and H. Henttonen. 1990. Demography and resource use by microtine rodents near Toolik Lake, Alaska, U.S.A. Arctic & Alpine Research 22:51–64.

Batzli, G. O., and C. Lesieutre. 1991. The influence of high quality food on habitat use by Arctic microtine rodents. Oikos 60:299–306.

Batzli, G. O., and C. Lesieutre. 1995. Community Organization of Arvicoline Rodents in Northern Alaska Community organization of arvicoline rodents in northern Alaska. Oikos 72:88–98.

Beauvais, G. P., and S. W. Buskirk. 1999. Modifying estimates of sampling effort to account for sprung traps. Wildlife Society Bulletin 27:39–43.

Berteaux, D., G. Gauthier, F. Domine, R. A. Ims, S. F. Lamoureux, E. Lévesque, and N. G. Yoccoz. 2017. Effects of changing permafrost and snow conditions on tundra wildlife: critical places and times. Arctic Science 3:65–90.

Bilodeau, F., G. Gauthier, and D. Berteaux. 2013. The effect of snow cover on lemming population cycles in the Canadian High Arctic. Oecologia 172:1007–1016.

Bilodeau, F., G. Gauthier, D. Fauteux, and D. Berteaux. 2014. Does lemming winter grazing impact vegetation in the Canadian Arctic? Polar Biology 37:845–857.

Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of Vegetative Cover to Cycles of Microtus Populations. Ecology 57:1043–1051.

Biuw, M., J. U. Jepsen, J. Cohen, S. H. Ahonen, M. Tejesvi, S. Aikio, P. R. Wäli, O. P. L. Vindstad, A. Markkola, P. Niemelä, and R. A. Ims. 2014. Long-term Impacts of Contrasting

Management of Large Ungulates in the Arctic Tundra-Forest Ecotone: Ecosystem Structure and Climate Feedback. Ecosystems 17:890–905.

Bret-Harte, M. S., M. C. Mack, G. R. Shaver, D. C. Huebner, M. Johnston, C. A. Mojica, C. Pizano, and J. A. Reiskind. 2013. The response of Arctic vegetation and soils following an unusually severe tundra fire. Philosophical Transactions of the Royal Society B: Biological Sciences 368.

Chen, Y., F. S. Hu, and M. J. Lara. 2020. Divergent shrub-cover responses driven by climate, wildfire, and permafrost interactions in Arctic tundra ecosystems. Global Change Biology 27:1–12.

Christie, K. S., J. P. Bryant, L. Gough, V. T. Ravolainen, R. W. Ruess, and K. D. Tape. 2015. The Role of Vertebrate Herbivores in Regulating Shrub Expansion in the Arctic: A Synthesis. BioScience 65:1123–1133.

Cole, R. F., and G. O. Batzli. 1979. Nutrition and Population Dynamics of the Prairie Vole, Microtus ochrogaster, in Central Illinois. Journal of Animal Ecology 48:455–470.

Collins, S. L., J. B. Nippert, J. M. Blair, J. M. Briggs, P. Blackmore, and Z. Ratajczak. 2021. Fire frequency, state change and hysteresis in tallgrass prairie. Ecology Letters 24:636–647.

Dahlgren, J., L. Oksanen, T. A. Oksanen, J. Olofsson, P. A. Hambäck, and Å. Lindgren. 2009. Plant defences to no avail? Responses of plants of varying edibility to food web manipulations in a low arctic scrubland. Evolutionary Ecology Research 11:1189–1203.

Dehn, M. M., R. C. Ydenberg, and L. M. Dill. 2017. Experimental addition of cover lowers the perception of danger and increases reproduction in meadow voles (Microtus pennsylvanicus). Canadian Journal of Zoology 95:463–472.

Desy, E. A. ., and C. F. Thompson. 1983. Effects of Supplemental Food on a Microtus pennsylvanicus Population in Central Illinois. Journal of Animal Ecology 52:127–140.

Duchesne, D., G. Gauthier, and D. Berteaux. 2011. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. Oecologia 167:967–980.

Ekerholm, P., L. Oksanen, T. A. Oksanen, and M. Schneider. 2004. The Impact of Short-Term Predator Removal on Vole Dynamics in an Arctic-Alpine Landscape. Oikos 106:457–468.

Forbes, K. M., P. Stuart, T. Mappes, K. S. Hoset, H. Henttonen, and O. Huitu. 2014. Diet quality limits summer growth of field vole populations. PLoS ONE 9:1–8.

Frost, G. V., R. A. Loehman, L. B. Saperstein, M. J. Macander, P. R. Nelson, D. P. Paradis, and S. M. Natali. 2020. Multi-decadal patterns of vegetation succession after tundra fire on the Yukon-Kuskokwim Delta, Alaska. Environmental Research Letters 15:025003.

García, Y., M. C. Castellanos, and J. G. Pausas. 2016. Fires can benefit plants by disrupting antagonistic interactions. Oecologia 182:1165–1173.

Gilg, O., B. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. Global Change Biology 15:2634–2652.

Gough, L., and D. R. Johnson. 2018. Mammalian herbivory exacerbates plant community responses to long-term increased soil nutrients in two Alaskan tundra plant communities. Arctic Science 4:153–166.

Gough, L., J. C. Moore, G. R. G. R. Shaver, R. T. Simpson, D. R. Johnson, R. David, J. C. Moore, and D. R. Johnson. 2012. Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. Ecology 93:1683–1694.

Gough, L., E. A. Ramsey, and D. R. Johnson. 2007. Plant herbivore interactions in Alaskan arctic tundra changewith soil nutrient availability. Oikos 116:407–418.

Grellmann, D. 2002. Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. Oikos 98:190–204.

Heim, R. J., A. Bucharova, D. Rieker, A. Yurtaev, J. Kamp, and N. Hölzel. 2019. Long-term effects of fire on Arctic tundra vegetation in Western Siberia. bioRxiv:756163.

Hu, F. S., P. E. Higuera, P. A. Duffy, M. L. Chipman, A. V. Rocha, A. M. Young, R. Kelly, and M. C. Dietze. 2015. Arctic tundra fires: natural variability and responses to climate change. Frontiers in Ecology and the Environment 13:369–377.

Huntly, N. J. 1991. Herbivores and the Dynamics of Communities and Ecosystems. Annual Review of Ecology and Systematics 22:477–503.

Ims, R. A., and E. Fuglei. 2005. Trophic Interaction Cycles in Tundra Ecosystems and the Impact of Climate Change. BioScience 55:311–322.

Jiang, Y., E. B. Rastetter, A. V. Rocha, A. R. Pearce, G. R. Shaver, and B. L. Kwiatkowski. 2015. Modeling carbon — nutrient interactions during the early recovery of tundra after fire. Ecological Applications 25:1640–1652.

Johnson, D. R., and L. Gough. 2013. Two arctic tundra graminoids differ in tolerance to herbivory when grown with added soil nutrients. Botany 91:82–90.

Joly, K., P. Bente, and J. Dau. 2007. Response of overwintering caribou to burned habitat in northwest Alaska. Arctic 60:401–410.

Jones, B. M., A. L. Breen, B. V. Gaglioti, D. H. Mann, A. V. Rocha, G. Grosse, C. D. Arp, M. L. Kunz, and D. A. Walker. 2013. Identification of unrecognized tundra fire events on the north slope of Alaska. Journal of Geophysical Research: Biogeosciences 118:1334–1344.

Jones, B. M., G. Grosse, C. D. Arp, E. Miller, L. Liu, D. J. Hayes, and C. F. Larsen. 2015. Recent Arctic tundra fire initiates widespread thermokarst development. Scientific Reports 5:1–13.

Jones, B. M., C. A. Kolden, R. R. Jandt, J. Abatzoglou, F. E. Urban, and C. D. Arp. 2009. Fire behavior, weather, and burn severity of the 2007 anaktuvuk river tundra fire, North Slope, Alaska. Arctic, Antarctic, and Alpine Research 41:309–316.

Jones, M. W., A. Smith, R. Betts, J. G. Canadell, I. C. Prentice, and C. Le Quéré. 2020. Climate change increases the risk of wildfires. Page Science Brief.

Jorgenson, M. T., Y. L. Shur, and E. R. Pullman. 2006. Abrupt increase in permafrost degradation in Arctic Alaska. Geophysical Research Letters 33:L02503.

Karlsen, S. R., J. U. Jepsen, A. Odland, R. A. Ims, and A. Elvebakk. 2013. Outbreaks by canopy-feeding geometrid moth cause state-dependent shifts in understorey plant communities. Oecologia 173:859–870.

Kasischke, E. S., and M. R. Turetsky. 2006. Recent changes in the fire regime across the North American boreal region - Spatial and temporal patterns of burning across Canada and Alaska. Geophysical Research Letters 33:L09703.

Klupar, I., A. V. Rocha, and E. B. Rastetter. 2021. Alleviation of nutrient co-limitation induces regime shifts in post-fire community composition and productivity in arctic tundra. Global Change Biology Advance on.

Korslund, L., and H. Steen. 2006. Small rodent winter survival: Snow conditions limit access to food resources. Journal of Animal Ecology 75:156–166.

Krebs, C. J. 2013. Population fluctuations in rodents. University of Chicago Press, Chicago.

Van Langevelde, F., C. A. D. . Van de Vijver, L. Kumar, J. Van de Koppel, N. De Ridder, J. Van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, P. H. T. Herbert, and M. Reitkerk. 2003. Effects of Fire and Herbivory on the Stability of Savanna Ecosystems. Ecology 84:337–350.

Lantz, T. C., S. V. Kokelj, S. E. Gergel, and G. H. R. Henry. 2009. Relative impacts of disturbance and temperature: Persistent changes in microenvironment and vegetation in retrogressive thaw slumps. Global Change Biology 15:1664–1675.

Lehtonen, J., and R. K. Heikkinen. 1995. On the recovery of mountain birch after Epirrita damage in Finnish Lapland, with a particular emphasis on reindeer grazing. Ecoscience 2:349–356.

Lybbert, A. H., and S. B. St. Clair. 2017. Wildfire and floral herbivory alter reproduction and pollinator mutualisms of Yuccas and Yucca moths. Journal of Plant Ecology 10:851–858.

Mack, M. C., M. S. Bret-Harte, T. N. Hollingsworth, R. R. Jandt, E. A. G. Schuur, G. R. Shaver, and D. L. Verbyla. 2011. Carbon loss from an unprecedented Arctic tundra wildfire. Nature 475:489–492.

McCarty, J. L., J. Aalto, V. V. Paunu, S. R. Arnold, S. Eckhardt, Z. Klimont, J. J. Fain, N. Evangeliou, A. Venäläinen, N. M. Tchebakova, E. I. Parfenova, K. Kupiainen, A. J. Soja, L. Huang, and S. Wilson. 2021. Reviews and syntheses: Arctic fire regimes and emissions in the 21st century. Biogeosciences 18:5053–5083.

McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annual Review of Entomology 43:107–27.

McGraw, J. B., and G. R. Shaver. 1982. Seedling density and seedling survival in Alaskan cotton grass tussock tundra. Ecography 5:212–217.

Myers-Smith, I. H., and D. S. Hik. 2013. Shrub canopies influence soil temperatures but not nutrient dynamics: An experimental test of tundra snow-shrub interactions. Ecology and Evolution 3:3683–3700.

Narita, K., K. Harada, K. Saito, Y. Sawada, M. Fukuda, and S. Tsuyuzaki. 2015. Vegetation and

Permafrost Thaw Depth 10 Years after a Tundra Fire in 2002, Seward Peninsula, Alaska. Arctic, Antarctic, and Alpine Research 47:547–559.

O'Connor, R. C., J. H. Taylor, and J. B. Nippert. 2020. Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland. Ecology 101:1–11.

Olofsson, J., H. Tømmervik, and T. V. Callaghan. 2012. Vole and lemming activity observed from space. Nature Climate Change 2:880.

Pauli, J. N., B. Zuckerberg, J. P. Whiteman, and W. Porter. 2013. The subnivium: A deteriorating seasonal refugium. Frontiers in Ecology and the Environment 11:260–267.

Pérez, J. H., H. E. Chmura, and J. S. Krause. 2018. Tundra avian community composition during recovery from the Anaktuvuk River Fire. International Journal of Wildland Fire 27:69–71.

Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Hoye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. Mcguire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. Van Der Wal, J. M. Welker, P. A. Wookey, N. M. Schmidt, P. Aastrup, and T. T. Høye. 2009. Ecological dynamics across the arctic associated with recent climate change. Science 325:1355–1358.

Racine, C. H., R. R. Jandt, C. Meyers, and J. Dennis. 2004. Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, U.S.A. Arctic, Antarctic, and Alpine Research 36:1–10.

Racine, C. H., L. A. Johnson, and L. A. Viereck. 1987. Patterns of vegetation recovery after tundra fires in northwestern Alaska, USA. Arctic & Alpine Research 19:461–469.

Raffaele, E., T. T. Veblen, M. Blackhall, and N. Tercero-bucardo. 2011. Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina.

Journal of Vegetation Science 22:59–71.

Ravolainen, V. T., K. A. Bråthen, N. G. Yoccoz, J. K. Nguyen, and R. A. Ims. 2014. Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. Journal of Applied Ecology 51:234–241.

Reid, D. G., F. Bilodeau, C. J. Krebs, G. Gauthier, A. J. Kenney, S. B. Gilbert, M. C. Y. Leung, D. Duchesne, and E. J. Hofer. 2012. Lemming winter habitat choice: a snow-fencing experiment. Oecologia 168:935–946.

Rocha, A. V., R. Appel, M. S. Bret-Harte, E. S. Euskirchen, V. G. Salmon, and G. R. Shaver. 2021. Solar position confounds the relationship between ecosystem function and vegetation indices derived from solar and photosynthetically active radiation fluxes. Agricultural and Forest Meteorology 298–299:108291.

Rocha, A. V., M. M. Loranty, P. E. Higuera, M. C. MacK, F. S. Hu, B. M. Jones, A. L. Breen, E. B. Rastetter, S. J. Goetz, and G. R. Shaver. 2012. The footprint of Alaskan tundra fires during the past half-century: Implications for surface properties and radiative forcing. Environmental Research Letters 7:044039.

Rocha, A. V., and G. R. Shaver. 2009. Advantages of a two band EVI calculated from solar and photosynthetically active radiation fluxes. Agricultural and Forest Meteorology 149:1560–1563.

Rocha, A. V., and G. R. Shaver. 2011a. Postfire energy exchange in arctic tundra: The importance and climatic implications of burn severity. Global Change Biology 17:2831–2841.

Rocha, A. V., and G. R. Shaver. 2011b. Burn severity influences postfire CO2 exchange in arctic tundra. Ecological Applications 21:477–489.

RStudio Team. 2019. R Studio: Integrated Development Environment for R. RStudio, Inc., Boston, MA.

Schuur, E. A. G., K. G. Crummer, J. G. Vogel, and M. C. MacK. 2007. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. Ecosystems 10:280–292.

Shaver, G. R., M. S. Bret-Harte, M. H. Jones, and J. F. Johnstone. 2001. Species Composition Interacts with Fertilizer to Control Long-Term Change in Tundra Productivity. Ecology 82:3163–3181.

Shaver, G. R., F. S. I. Chapin, and B. L. Gartner. 1986. Factors Limiting Seasonal Growth and Peak Biomass Accumulation in Eriophorum Vaginatum in Alaskan Tussock Tundra. Journal of Ecology 74:257–278.

Shaver, G. R., and F. S. Chapin III. 1995. Long-Term Responses to Factorial , NPK Fertilizer Treatment by Alaskan Wet and Moist Tundra Sedge Species. Ecography 18:259–275.

Sikes, R. S., J. A. Bryan, D. Byman, B. J. Danielson, J. Eggleston, M. R. Gannon, W. L. Gannon, D. W. Hale, B. R. Jesmer, D. K. Odell, L. E. Olson, R. D. Stevens, T. A. Thompson, R. M. Timm, S. A. Trewhitt, and J. R. Willoughby. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Sistla, S. A., J. C. Moore, R. T. Simpson, L. Gough, G. R. Shaver, and J. P. Schimel. 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497:615–617.

Sturm, M., J. P. McFadden, G. E. Liston, F. S. I. Chapin, C. H. Racine, and J. Holmgren. 2000. Snow-shrub interactions in Arctic Tundra: A hypothesis with climatic implications. Journal of Climate 14:336–344.

Taitt, M. K., J. H. W. Gipps, C. J. Krebs, and Z. Dundjerski. 1981. The effect of extra food and cover on declining populations of Microtus townsendii. Canadian Journal of Zoology 59:1593–1599.

Taitt, M. K., and C. J. Krebs. 1981. The Effect of Extra Food on Small Rodent Populations: II. Voles (Microtus townsendii). Journal of Animal Ecology 50:125–137.

Tast, J. 1972. Annual variations in the weights of wintering root voles , Microtus oeconomus , in relation to their food conditions. Annales Zoologici Fennici 9:116–119.

Treberg, M. A., K. L. Edwards, and R. Turkington. 2010. Voles are attracted to fertilizer in field experiments. Arctic, Antarctic, and Alpine Research 42:113–116.

Tuomi, M., S. Stark, K. S. Hoset, M. Väisänen, L. Oksanen, F. J. A. Murguzur, H. Tuomisto, J. Dahlgren, and K. A. Bråthen. 2019. Herbivore Effects on Ecosystem Process Rates in a Low-Productive System. Ecosystems 22:827–843.

Vindstad, O. P. L., J. U. Jepsen, M. Ek, A. Pepi, and R. A. Ims. 2019. Can novel pest outbreaks drive ecosystem transitions in northern - boreal birch forest ? Journal of Ecology 107:1031–1530.

Wan, H. Y., A. C. Rhodes, and S. B. St. Clair. 2014. Fire severity alters plant regeneration patterns and defense against herbivores in mixed aspen forests. Oikos 123:1479–1488.

Wein, R. W., and L. C. Bliss. 1973. Changes in Arctic Eriophorum Tussock Communities Following Fire. Ecology 54:845–852.

West, S. D. 1979. Ecological Effects of the Wickersham Dome Fire Near Fairbanks Alaska. Page Pacific Northwest Forest and Range Experiment Station USDA & Forest Service.

West, S. D. 1982. Dynamics of Colonization and Abundance in Central Alaskan Populations of the Northern Red-Backed Vole, Clethrionomys rutilus. Journal of Mammalogy 63:128–143.

Ylänne, H., S. Stark, and A. Tolvanen. 2015. Vegetation shift from deciduous to evergreen dwarf shrubs in response to selective herbivory offsets carbon losses: Evidence from 19 years of warming and simulated herbivory in the subarctic tundra. Global Change Biology 21:3696–3711.

Young, A. M., P. E. Higuera, P. A. Duffy, and F. S. Hu. 2017. Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. Ecography 40:606–617.

Table 1. Tussock characteristics and researcher mobility at burned and unburned sites. Values represent averages (+/- Standard Error). With the exception of rhizome biomass ($t_{36} = 1.35$, $p = 0.18$) all comparisons between the burned and unburned site were significant: density: $t_{285} = -5.2$, $p < 0.001$; height: $t_{146.6} = 10.56$, $p < 0.001$; diameter $t_{180.4} = 4.47$, $p < 0.001$; mobility: $t_4 = 4.94$, $p = 0.007$. Diameter was calculated from 79 tussocks at the burned site and 111 tussocks at the unburned site.

Site	Tussock		
	* Density^{-1} m^2	Rhizome biomass (g/m^2)	Diameter (cm)
Burned	10.8 +/- 0.3	548 +/- 85	23.8 +/- 0.7
Unburned	12.9 +/- 0.2	404 +/- 65	19.7 +/- 0.6

* Total density includes live and dead tussocks. Live tussocks represented 7.9 (+/- 0.3) per meter squared at the burned, compared to 12.2 (+/- 0.2) at the unburned site.

Figure 1. (a) Two-band EVI from 2008-2019 at the burned and unburned site, calculated from incoming and outgoing solar and photosynthetically active radiation (PAR) +/- SE, as described by Rocha and Shaver 2009. (**b**) Burned tussock mounds in 2008, 1 year following the Anaktuvuk River fire. (**c**) Tussocks at the burned site pictured in 2019, 12 years after the fire.

Figure 2. LAI and vegetation height at the burned and unburned site. **(a)** Average LAI by growth form +/- SE taken from 10x40cm quadrats (n=20). Forb and graminoid LAI were significantly greater at the burned than the unburned site (forb: W= 297.5, p= 0.008; graminoid: W= 286, p=0.02), while deciduous shrub LAI followed a similar although non-significant pattern (W=240.5, p=0.26; but see Klupar et al. 2021). No difference was observed in evergreens (W=163, p= 0.3). **(b)** Mean vegetation (ground to canopy) height by growth form of the tallest vegetation-pin hits +/- SE, averaged per point frame replicate (n = 5). Graminoids include heights of tussock tillers in addition to other graminoid species.

Figure 3. Tussock height and nitrogen content at the burned and unburned site. (**a**) Illustration of tussock height as measured from "mound", excluding tillers, to ground surface, which often comprised of moss at the unburned site. (**b**) Comparison of average tussock heights +/- SE at burned (n = 79) and unburned (n = 111) sites. (**c**) Tussock rhizome nitrogen biomass +/- SE. Values were calculated using average rhizome biomass m^{-2} (Table 1; n=20), and percent rhizome nitrogen estimates from a pooled sample (inset plot) consisting of n=6 and n=8 tussocks at the burned and unburned sites. Differences in rhizome nitrogen biomass were significant between sites (W=344, p < 0.001).

Figure 4. Differences in rodent herbivore density and activity at the burned and unburned site. **(a)** Tundra vole captures per 100 trap nights over 4 years (spanning 7-12 years post-fire). Differences in abundance between sites were significant ($t_3 = 4.45$, $p = 0.02$). **(b)** Average rodent sign (activities, e.g., latrines, nests) +/- SE m^{-2} 12 years post-fire. Differences in activities between sites were significant ($W = 2211.5$, $p < 0.001$).

Figure 5. Differences in tussock mortality between sites, and herbivore impacts on tussock biomass at the burned site. (a) Average tussock mortality +/- SE due to herbivory, fire, and natural causes at the burned and unburned site. At the burned site, 73% of all tussocks counted were live, and 27% were dead (n = 1,628). At the unburned site 0.1% of tussocks were dead, and only natural mortality was observed (n = 1,940). (b) Average biomass of tussocks from the burned site with (grazed) and without (ungrazed) rodent herbivory as measured per tissue type. Grazed values represent average biomass +/- SE calculated from 18 whole plucked tussocks with evidence of major vole herbivory while ungrazed values represent averages from 15 tussocks; calculated from 2 whole plucked tussocks, 5 tussock subsections, and 8 were based on allometric equations using height and diameter.