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Impacts of introduced *Rangifer* on ecosystem processes of maritime tundra on subarctic islands

MARK A. RICCA,[1,2,4,†] A. KEITH MILES,[1,2] DIRK H. VAN VUREN,[2] AND VALERIE T. EVINER[3]

[1] *U.S. Geological Survey, Western Ecological Research Center, University of California,*
One Shields Avenue, Davis, California 95616 USA
[2] *Department of Wildlife, Fish and Conservation Biology, University of California, Davis, California 95616 USA*
[3] *Department of Plant Sciences, University of California, Davis, California 95616 USA*

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Abstract. Introductions of mammalian herbivores to remote islands without predators provide a natural experiment to ask how temporal and spatial variation in herbivory intensity alter feedbacks between plant and soil processes. We investigated ecosystem effects resulting from introductions of *Rangifer tarandus* (hereafter "*Rangifer*") to native mammalian predator- and herbivore-free islands in the Aleutian archipelago of Alaska. We hypothesized that the maritime tundra of these islands would experience either: (1) accelerated ecosystem processes mediated by positive feedbacks between increased graminoid production and rapid nitrogen cycling; or (2) decelerated processes mediated by herbivory that stimulated shrub domination and lowered soil fertility. We measured summer plant and soil properties across three islands representing a chronosequence of elapsed time post-*Rangifer* introduction (Atka: ~100 yr; Adak: ~50; Kagalaska: ~0), with distinct stages of irruptive population dynamics of *Rangifer* nested within each island (Atka: irruption, K-overshoot, decline, K-re-equilibration; Adak: irruption, K-overshoot; Kagalaska: initial introduction). We also measured *Rangifer* spatial use within islands (indexed by pellet group counts) to determine how ecosystem processes responded to spatial variation in herbivory. Vegetation community response to herbivory varied with temporal and spatial scale. When comparing temporal effects using the island chronosequence, increased time since herbivore introduction led to more graminoids and fewer dwarf-shrubs, lichens, and mosses. Slow-growing *Cladonia* lichens that are highly preferred winter forage were decimated on both long-term *Rangifer*-occupied islands. In addition, linear relations between more concentrated *Rangifer* spatial use and reductions in graminoid and forb biomass within islands added spatial heterogeneity to long-term patterns identified by the chronosequence. These results support, in part, the hypothesis that *Rangifer* population persistence on islands is facilitated by successful exploitation of graminoid biomass as winter forage after palatable lichens are decimated. However, the shift from shrubs to graminoids was expected to enhance rates of nitrogen cycling, yet rates of net N-mineralization, NH_4^+ pools, and soil $\delta^{15}N$ declined markedly along the chronosequence and were weakly associated with spatial use within islands. Overall plant and soil patterns were disrupted but responded differently to intermediate (50 yr) and long-term (100 yr) herbivory, and were correlated with distinct stages of irruptive population dynamics.

Key words: Alaska; Aleutian; alternative state; caribou; irruption; isotope; mineralization; nitrogen; plant; *Rangifer tarandus*; reindeer; soil.

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[4] Present address: U.S. Geological Survey, Western Ecological Research Center, 800 Business Park Drive, Suite D, Dixon, California 95620 USA.
† **E-mail:** mark_ricca@usgs.gov

INTRODUCTION

Herbivores strongly impact ecosystems with weak top-down control (Hairston et al. 1960, Oksanen and Oksanen 2000). It follows that nonnative herbivory in ecosystems lacking predators represents a perturbation that can disrupt feedbacks that maintain a particular ecosystem state (Scheffer et al. 2001, Suding et al. 2004, Standish et al. 2014) by altering plant community structure that then shift patterns of nutrient cycling (Jefferies et al. 1994, Hobbs 1996, Pastor and Cohen 1997, Ritchie et al. 1998, Singer and Schoenecker 2003, Bardgett and Wardle 2010). Two common responses of ecosystems to herbivory are "accelerated" and "decelerated" ecosystem processes (sensu Ritchie et al. 1998, Singer and Schoenecker 2003, Bardgett and Wardle 2010). Accelerated processes are more likely in fertile ecosystems, whereby sustained herbivory increases dominance of herbivory-tolerant plants with high tissue quality (e.g., low foliar C:N ratios), such as graminoids. A combination of highly labile plant litter and large inputs of readily decomposable plant fiber in herbivore waste then enhances soil nutrient cycling that further stimulates aboveground productivity of plants with high tissue quality (Hobbs 1996, Bardgett and Wardle 2010). In contrast, decelerated processes are more likely in low fertility ecosystems, whereby intense herbivory decreases the prevalence of palatable but herbivory-intolerant plants such as forbs and leaves of deciduous shrubs. These palatable plants are replaced by chemically defended functional types such as evergreen shrubs. Recalcitrant litter and less nitrogenous waste from fewer herbivores slow decomposition rates, and a feedback that maintains low productivity and nutrient availability ensues (Ritchie et al. 1998, Singer and Schoenecker 2003, Bardgett and Wardle 2010). Importantly, processes can also shift from accelerating to decelerating within foraging patches when herbivory intensity surpasses some threshold (e.g., herbivore optimization) (McNaughton 1979, 1983, Hobbs 1996).

Tundra ecosystems commonly experience herbivory by caribou and reindeer (*Rangifer tarandus,* hereafter "*Rangifer*" when referring to both ecotypes), which have a circumpolar distribution. The strong nitrogen limitation common to tundra ecosystems (Shaver and Chapin 1986) should typically create environmental conditions that favor a deceleration of ecosystem processes when *Rangifer* herbivory is temporally and spatially intense, yet accelerating and decelerating processes have been described. *Rangifer* herbivory can promote graminoid dominance by adding high inputs of nitrogenous waste and indirectly increasing soil temperatures via reduction of thick moss and lichen mats, resulting in accelerating processes (Jefferies et al. 1994, Post and Klein 1996, Olofsson et al. 2001, 2004, van der Wal and Brooker 2004, van der Wal 2006, Post and Pedersen 2008, Olofsson 2009). Some studies even suggest that intense grazing maintains a graminoid-dominated state with a carrying capacity higher than that of the preceding moss and lichen dominated state (Olofsson et al. 2004, van der Wal 2006), and similar reasoning has been proposed for the maintenance of a graminoid tundra state by mega-herbivores during the Pleistocene (Zimov et al. 1995). In contrast, *Rangifer* herbivory could limit biomass accumulation of palatable tundra plants and drive an increase in chemically defended plants such as evergreen shrubs that can occur when arctic mammalian herbivores graze in nutrient-poor habitats (Bryant et al. 1983, Jefferies et al. 1994, Pastor and Cohen 1997). *Rangifer* have also evolved to utilize certain lichen taxa (particularly *Cladonia*) to meet energetic demands in winter (Bergerud 2000), yet lichens grow very slowly and are depleted easily with high grazing intensity (Klein 1968, Klein and Shulski 2009). These decelerated processes would likely decrease *Rangifer* carrying capacity (Oksanen and Oksanen 2000, Brathen et al. 2007, Hansen et al. 2007). Clearly, the impacts of *Rangifer* on ecosystem processes are context dependent.

Island introductions as natural experiments

Introductions of ruminants to islands lacking predators or other mammalian herbivores provide useful natural experiments (Oksanen et al. 2010) to examine how herbivory alters plant communities and nutrient cycling, which subsequently influences the carrying capacity and persistence of the introduced herbivore. Yet, no studies to our knowledge have examined how *Rangifer* herbivory on islands alters nitrogen cycling, particularly in relation to indirect changes to plant functional traits (e.g., foliar C:N ratios, herbivory tolerance) that influence litter quality, and direct inputs of nitrogenous waste from excrement. In addition, maritime tundra associated with subarctic islands does not experience extreme low temperatures and lacks permafrost soils, so ecosystem processes driving nitrogen cycling (e.g., decomposition rates) may respond more rapidly to direct and indirect effects of herbivory relative to those occurring on arctic islands. Predictions are made even more difficult given contrasting results from mainland tundra studies and the limited number of insular tundra studies. For example, *Rangifer*-driven increases in graminoid biomass at the expense of slower growing plant functional types (Olofsson et al. 2001, 2004, van der Wal 2006, Olofsson 2009) fits within the accelerated framework. However, nitrogen limitation and spatial constraints imposed by island living might lead to strong decelerating processes that limit accumulation of graminoids and other palatable functional types and favor unpalatable taxa and lead to lower soil fertility (Oksanen and Oksanen 2000, Hansen et al. 2007).

Perhaps most importantly, whether ecosystem processes shift in an accelerated or decelerated direction can be influenced, in part, by how long *Rangifer* have existed postintroduction and their stage of population growth (i.e., irrupting, declining, postirruption) (Klein 1968, 1987, Leader-Williams 1988). Population dynamics of unmanaged *Rangifer* on islands are well described and generally follow a four-stage irruptive growth model described by Riney (1964) and Caughley (1970). An irruption in population size after release leads to an overshoot of carrying capacity, which is followed by a density-dependent decline in population size and ultimate re-equilibration to a lower carrying capacity. The initial irruption is fueled by large quantities of accumulated forage biomass, and overexploitation of this "surplus forage", particularly in winter, drives population crashes that can lead to extinction (Mysterud 2006, Gross et al. 2010). However, functional traits of insular vegetation can alter the amplitude of irruptions and crashes (Mysterud 2006, Gross et al. 2010). Large standing crops of slow-growing *Cladonia* are depleted rapidly at high grazing densities, so the persistence of insular *Rangifer* populations may be related to the availability of herbivory-tolerant graminoids that replace lichens as a winter-food source (Klein 1968, 1991, Leader-Williams 1988). This mechanism (or lack thereof) has been illustrated by a few highly influential case studies of *Rangifer* occupying islands with arctic and subantarctic climates. Reindeer populations on the Bering Sea islands of St. Matthew (Klein 1968, 1987), St. Paul, and St. George (Scheffer 1951) famously perished after <50 yr of existence due in part to the decimation of large standing crops of lichens coupled with catastrophic winter weather. In contrast, reindeer on South Georgia Island in the South Atlantic have persisted for nearly a century after exhausting lichens, via reliance on native tussock and eventually exotic graminoids that could withstand high levels of grazing pressure (Leader-Williams 1988). Importantly, the Riney–Caughley model predicts an eventual decline in herbivore numbers due to reduced carrying capacity near stage 4. Although *Rangifer*-driven changes to insular ecosystems (e.g., shift to graminoids) may reduce population vulnerability to stochastic events and enhance persistence probability, these changes on island tundra may not have the same effect of enhancing carrying capacity that has been proposed for mainland tundra (van der Wal 2006).

Rangifer introductions to the Aleutian archipelago

Introductions of *Rangifer* to large (>700 km^2) islands in the Aleutian archipelago of Alaska provide an unexplored natural experiment to examine how nonnative herbivores accelerate or decelerate ecosystem processes. In addition, variable timing of introductions to specific islands and subsequent management practices represent a useful chronosequence that allows examination of how effects of herbivory related to elapsed time postintroduction may accelerate or decelerate ecosystem processes and trigger shifts toward possible alternative states (Fig. 1). The chronosequence comprises three islands with "extensive" (Atka, ~100 yr), "intermediate" (Adak, ~50 yr), and "nominal" (Kagalaska, ~0 yr) histories of herbivory. Importantly, unique stages of irruptive population dynamics are nested within each island. *Rangifer* on Atka have not been subjected to strong pressure from

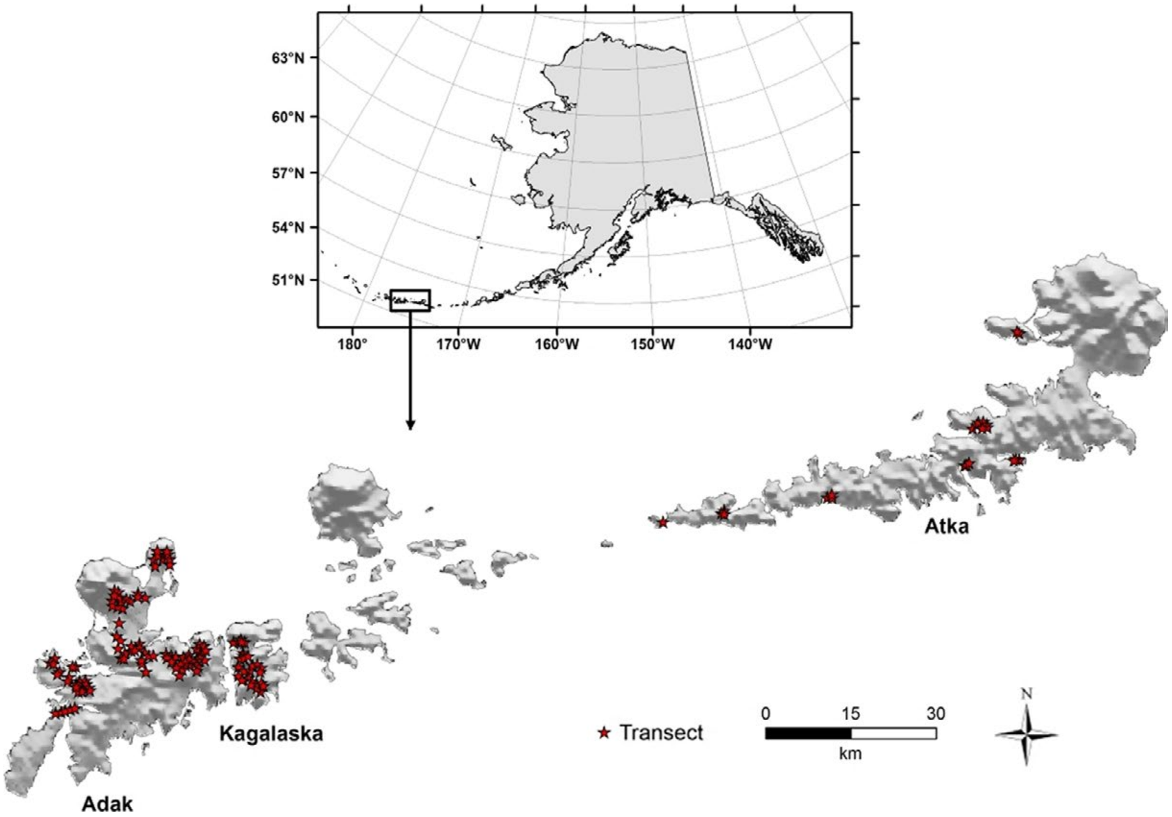

Fig. 1. Map of islands in the Aleutian archipelago of Alaska enduring nominal (Kagalaska, ~0 yr), intermediate (Adak, ~50 yr), and extensive (Atka, ~100 yr) history of introduced *Rangifer* herbivory, and distribution of 400 m transects sampled in this study during the summers of 2010 and 2011.

managed hunter harvest or herding activities over their history, so they have likely undergone all four stages of Riney–Caughley model irruptive growth that nearly all surviving populations of introduced island *Rangifer* have followed (Leader-Williams 1988, Tyler 2010). In contrast, caribou had only recently invaded Kagalaska at the time of our study, so divergence among ecosystem processes on Atka compared to Kagalaska should represent the outcome of long-term herbivory. *Rangifer* on Adak represent an approximate 50-yr history of herbivory, but were kept at relatively low density by managed hunting for ~35 yr before undergoing a period of exponential growth following relaxation of hunting pressure (Ricca et al. 2014). Thus, Adak may represent more transient effects given its intermediate history of herbivory, but the recent period of exponential growth could also shift overall patterns of ecosystem processes similar to those measured on Atka (Fig. 1).

We measured several ecosystem structure and function variables likely to be impacted by *Rangifer* along the three-island chronosequence while accounting for variation in spatial use within islands, and asked how *Rangifer* herbivory accelerated or decelerated changes in ecosystem processes relative to stages of irruptive population dynamics. We predicted that accelerated ecosystem processes should trigger a shift toward a graminoid state that favors the persistence of *Rangifer* at high abundance and enhances nutrient cycling. Alternatively, spatial constraints to movement and dispersal imposed by an island would lead to a deceleration of ecosystem processes that ultimately shifts *Rangifer* grazed islands toward a state of lower productivity capable of supporting fewer animals over time.

METHODS

Study area

Atka, Adak, and Kagalaska Islands are located in the Andreanof group of the central Aleutian archipelago at approximately 51.5° N, 176.5° W. Atka is located 70 km to the east of Kagalaska, while Kagalaska is separated from Adak to the west by a narrow (~1 km) and turbulent strait. Small human communities (<300 people) exist on Adak and Atka where land ownership is mixed between Alaska Native Corporation inholdings and wilderness managed by the USFWS Alaska Maritime National Wildlife Refuge (AMNWR). All of Kagalaska is managed by the AMNWR as wilderness and has no human habitation.

Similar geological histories, climates, and plant–soil characteristics across islands in the archipelago provide a setting conducive for natural experiments that examine effects of introduced perturbations (Croll et al. 2005, Maron et al. 2006). Islands in our study are large (Atka = 1048 km^2, Adak = 725 km^2, Kagalaska = 116 km^2) with rugged, mountainous terrain formed by Pleistocene glaciation (Fraser and Synder 1959). Unlike the Bering Sea islands where introduced reindeer perished, winter sea-ice remains well to the north of the Aleutians. Hence, climates and plant communities are classified as maritime. Summers are characterized by cool (5–10 °C) temperatures and persistent fog and rain, while winter temperatures fluctuate near 0 °C and cyclonic storms occur commonly. Annual precipitation is roughly 160 cm and there is no consistent prevailing wind direction. The plant growing season is relatively short and occurs primarily from June through August. Soils are of volcanic origin and classified as Typic Haplocryands on all islands (NRCS 2013). Soil fertility is generally low in the absence of allochthonous nutrient subsidies (Croll et al. 2005, Maron et al. 2006). Land mammals are not native to any of the islands in our study.

Walker (2000) classified maritime tundra throughout the Aleutians as "oceanic herb – dwarf-shrub". Plant communities are compositionally similar throughout the Andreanof Islands, with low beta-diversity relative to those found on both the Asian and Alaskan mainland (Hultén 1968, Heusser 1978, Talbot et al. 2010), and are typically graminoid or dwarf-shrub dominated. Graminoid-dominated wet and alpine meadows are characterized by several species of grasses (e.g., *Agrostis* sp. *Calamagrostis canadensis, C. nutkaensis, Deschampsia* sp. *Festuca* sp., *Leymus mollis*), sedges (e.g., *Carex anthoxanthea, C. kelloggii., C. macrochaeta, C. pluriflora, Eriophorum* sp., *Trichophorum caespitosum*), rushes (e.g., *Luzula* sp. *Juncus* sp.), and forbs (e.g., *Anemone narcissiflora, Arnica unalaschcensis, Epilobium* sp. *Erigeron peregrinus, Geranium erianthum, Plantago macrocarpa, Platanthera* sp.). Dwarf-shrub dominated upland heaths and fellfields typically comprise evergreen (e.g., *Empetrum nigrum, Phyllodoce aleutica, Loiseleuria procumbens*) and deciduous dwarf-shrubs (e.g., *Vaccinium uliginosum, Salix* sp.), along with fruiticose lichens (e.g., *Cladonia rangiferina, Cetraria islandica, Thamnolia vervicularis*) and mosses. Tall shrubs and trees are nonexistent.

Island chronosequence

Reindeer originating from Siberia were introduced to Atka in 1914 to provide a herding-based economy and subsistence for Alaska Natives on the island (Veltre and Veltre 1983, Swanson and Barker 1992). Although a robust time series for this population does not exist, the population has been roughly estimated at 2500–3500 (2.4–3.4 km^{-2}) animals in 1973 and at 2000 animals (2.0 km^{-2}) by 1990 (Veltre and Veltre 1983, Swanson and Barker 1992), and recent surveys of shoreline habitats conducted by boat enumerated 236 animals during 2011 (J.C. Williams, *personal communication*), which indicated that reindeer were still common on the island. Reindeer herding was never developed into a sustainable economy, and <100 animals are thought to be killed by hunters per year. Hence, we assumed that Atka reindeer have likely completed at least one entire four-stage Riney–Caughley irruption, which is likely robust within the context of our study. On Adak, 23 caribou from mainland Alaska were transplanted during the late 1950s in an effort to provide hunting and subsistence opportunities for military personnel stationed on the island (Jones 1966). Regulated hunting kept the population at relatively low density through the early 1990s. The closure of the military base in the mid-1990s contributed to a dramatic decline in hunter harvest that fueled a threefold increase through at least 2005. However, population growth had slowed to resemble logistic growth by 2012, and population size was estimated at 2880 animals (4.0 km^{-2}). This pattern was likely related to intensifying density-dependent regulation and a new increase in hunting pressure (Ricca et al. 2014). Ecological differences between free-ranging reindeer on Atka and caribou on Adak are trivial, and higher relative densities on Adak compared to Atka fit the four-stage model.

We assumed that ecosystem processes on our "pseudocontrol" island of Kagalaska approximated conditions without *Rangifer*. Kagalaska was thought to have been caribou-free at the start of our study (Williams and Tutiakoff 2005), but the nascent stages of an invasion of caribou from Adak were detected during our study (Ricca et al. 2012, 2014). Sampling of another neighboring island to serve as a true *Rangifer*-free control was not logistically possible, yet the total number of animals and amount of sign detected on Kagalaska across all sampling periods of our study was miniscule compared to what we observed on Adak and Atka (Ricca et al. 2012, see Results). Hence, Kagalaska represented surplus forage conditions following initial release in accordance with the Riney–Caughley model, so we classified it accordingly as enduring a "nominal" history of herbivory.

Index of Rangifer spatial use

Variation in *Rangifer* spatial use within islands was indexed by the number of fecal pellet groups encountered along random 400 m transects (~1 m wide) sampled for ecosystem process measurements (see *Sampling Design* below). Pellet group counts provide an index for relative but not absolute abundance, and they are used commonly to assess broad patterns of spatial use by large herbivores (Weckerly and Ricca 2000, Forsyth et al. 2007) and relations between ruminant grazing intensity and variation in ecosystem processes (Frank and Evans 1997, van der Wal and Brooker 2004). An experimental study of fecal decomposition rates conducted on Adak during summer and fall of 2012 indicated that feces persisted in the environment long enough to reliably index *Rangifer* use during our summer transect surveys, but decomposed fast enough so that the majority (i.e., >50%) of excreted plant material had re-entered the terrestrial nitrogen cycle by the beginning of winter (Ricca 2013).

Sampling design

Plant and soil sampling occurred during the peak of the growing season in 2010 (4 August–30 August) and 2011 (17 July–20 August). Sampling occurred on Adak (intermediate history) and Kagalaska (nominal) during 2010 and 2011, whereas Atka (extensive) was sampled only in 2011. At all islands, we measured ecosystem processes along the same 400 m linear transects sampled for pellet counts, which comprised five, 1 m^2 plots spaced 100 m apart (Fig. 1). Distances between transects averaged 824 m (SD = 234 m, range: 207–1824 m) across all islands. Areas within 500 m of the ocean were excluded from sampling on all islands to minimize the confounding influence of marine-derived nutrient inputs (e.g., salt spray, seabird guano) (Maron et al. 2006). Transect sampling was random across all islands, but the type of random sampling differed among island for biological and logistical reasons. Field facilities were based on Adak, so sampling was more frequent there compared to Kagalaska, which was only reachable by a small skiff on infrequent calm days. Atka was only accessible by a large ship. We stratified Adak into four areas that corresponded roughly to long-term patterns of caribou density during the summer months (Ricca et al. 2014): north-side (low density), island center (moderate density), and east and west sides (high density). Kagalaska was stratified into three areas on the northwest, central, and south-central portions of the island to ensure broad spatial coverage that was comparable to the other islands sampled. We then overlaid a grid of 0.5 ha cells onto a GIS map and obtained the mid-point coordinates for each cell. Coordinates from stratified areas were then randomly sorted, and the top 20% were put into a pool of possible transect starting points. Choice of the actual starting point depended on accessibility (e.g., cliff faces, hiking or boating distance relative to time of day and current weather conditions), but all possible locations represented areas potentially used by caribou. We accessed Atka during August 2011 via the

AMNWR research vessel *Tiglax* that was conducting surveys unrelated to our work. Consequently, sampled areas needed to be opportunistic, which precluded the use of a predetermined stratified-random pool of start points. Instead, a random direction and distance for transect starting points was determined in the field after ship drop-off. Despite these limitations, we were able to sample transects across six distinct watersheds across the western side of Atka.

Topographic variables (elevation, slope, and aspect) and habitat type (meadow or heath) were recorded for all plots sampled within transects. Elevation was measured by GPS, and slope and aspect by hand-held clinometer and compass. We sampled elevations ranging from 20 to 360 m on all islands to encompass low elevations used by *Rangifer* during winter where snow cover is less deep, along with high elevation areas (>250 m) used more frequently toward the end of the summer (M.A. Ricca, *personal observation*). An additional 38 plots were sampled at elevations ranging from 360 to 540 m on Adak where a road network enabled quicker access to high elevation (>250 m) sites. We classified all plots in the field into two broad habitat variables based on the abundance of characteristic taxa similar to those described by Talbot et al. (2010). Meadow habitats comprised mesic meadows, wet snowbed meadows, and mires, whereas heath habitats comprised sites dominated by evergreen and deciduous shrubs, as well as infrequently encountered fellfields. Plots were spread across all islands between heath (33–41%) and meadow (59–67%) habitats. We quantified plant species presence–absence (typically to genus) within all 1 m^2 plots, and then verified the validity of habitat classifications in the field by conducting a nonmetric multidimensional scaling (NMS) ordination on Beal's-smoothed presence–absence data (McCune and Grace 2002). A three-dimensional solution explained 94% of the variation in the species matrix, and indicated separation of meadow and heath plots along species gradients in the ordination space.

Ecosystem structure measurements

Ecosystem structure was estimated in all 1 m^2 plots along each transect by quantifying: (1) biomass of graminoid, forb, and dwarf-shrub functional types; (2) percent horizontal cover of lichen and moss functional types; (3) depth of the dwarf-shrub mat; and (4) percent horizontal cover for a subset of *Rangifer* forage taxa with varying levels of palatability. Specific methods for each estimate are as follows.

Measures of percent horizontal cover and plant height were used to estimate biomass of graminoids, forbs, and dwarf-shrubs within each plot. We measured percent horizontal cover of each functional type using ocular estimates of Daubenmire cover classes that could overlap each other (i.e., total plant cover could exceed 100%), and plant height as the highest point of intersection on a ruler at nine roughly equidistant locations within each plot. We then measured percent horizontal cover and plant height within a subset of 0.2 m^2 plots for graminoids (n = 24), forbs (n = 106), and shrubs (n = 90), followed by clipping and sorting all live leaves of graminoids, forbs, and dwarf-shrubs, and oven-drying for at least 48 h at 60 °C to obtain a constant dry-weight biomass. We used AIC_c model selection to determine the best multiple regression model from a balanced set of eight candidate models to estimate biomass ($\log_e$ transformed) for each of the three functional groups. Predictor variables comprised additive combinations of linear and quadratic effects for average plant height measurements and cover class mid-points within the 0.2 m^2 plots. Biomass was best explained by cover + height + height^2 for graminoids (R^2 = 0.84), cover + cover^2 + height + height^2 for forbs (R^2 = 0.76), and cover + cover^2 + height for shrubs (R^2 = 0.80). We then used the parameter coefficients from the top model for each functional type to predict dry-weight biomass (g/m^2) at the 1 m^2 scale using cover class mid-point and average heights measured at the same 1 m^2 plot scale. We did not estimate biomass for lichens and mosses, and instead report percent horizontal cover based on Daubenmire cover class mid-points for these functional types.

The depth of the dwarf-shrub mat was measured as the average distance along a ruler from the bottom of the photosynthetic vegetation to the top of the organic soil layer measured at the same nine locations measured for plant height within each plot 1 m^2 plot. Dwarf-shrubs, especially *Empetrum*, can form deep and "spongy" mats of leafless stoloniferous branches intertwined with mosses, lichen, and leaf litter that can be more extensive than the photosynthetic portion. We reasoned that deep dwarf-shrub mats reduce soil temperatures and available light in a manner similar to lichen- and moss-mats in arctic tundra (van der Wal and Brooker 2004), and compaction of the mat by caribou hoof action and direct herbivory could create warmer soil conditions more conducive for graminoid growth.

We used mid-points of Daubenmire cover classes to estimate percent horizontal cover for *Rangifer* forage taxa that vary in quality and tolerance to herbivory (Skoog 1968, Jefferies et al. 1994). These data were only collected during 2011. Species representing graminoid taxa were divided into grasses (mostly *Calamagrostis* sp., *Festuca* sp., *Agrostis* sp.) and sedges (*Carex* sp.). Sedges are generally more palatable than grasses during the summer months (Klein 1990). Less palatable evergreen dwarf-shrubs mostly comprised *Empetrum nigrum* and evergreen ericoids (e.g., *Phyllodoce aleutica, Loiseleuria procumbens*), whereas more palatable deciduous dwarf-shrubs mostly comprised *Vaccinium uliginosum*, *Salix* sp., and *Cornus suecica. Cladonia* lichens (i.e., *C. rangiferina*, *C. stellaria*) represented a highly preferred winter forage taxa, while non-*Cladonia* lichens comprised less palatable fruiticose (e.g., *Thamnolia vervicularis*) and crustose lichens.

Soil and plant nitrogen

We measured soil and plant nitrogen processes within three plots (first, third, and last) along each transect. Soils were sampled in 2011, whereas leaf samples were collected in 2010 and 2011. Within each plot, three soil samples (including organic and mineral horizons) were collected at depth of 12 cm within the root zone using a 2.5 cm diameter corer in each plot, composited, and refrigerated for a maximum of 4 d before processing. Leaves from 20 to 30 individual plants from commonly encountered *Rangifer* forage taxa were collected within a 15 m maximum radius of each plot. Perennial grasses (*Calamagrostis* sp.), sedges (*Carex pluriflora* or *C. macrochaeta*), and forbs (*Anemone narcissiflora*) were collected at all islands. Leaf samples were sorted by taxa, placed in paper bags, and oven-dried at 40–50 °C within 4 d of collection. Using these soil and leaf samples, we estimated: (1) potential rates of net N-mineralization, inorganic-N pool size, and % nitrification; (2) foliar %C, %N, and natural abundance of nitrogen stable isotopes (δ^{15}N); and (3) soil %C, %N, and δ^{15}N.

Potential net rates of N-mineralization and inorganic-N pool sizes were measured in field moist soil samples passed through a 2 mm mesh sieve and homogenized. We extracted inorganic-N from a 5 g subsample of soil at the time of collection (t) by adding 25 mL of 2 mol/L KCl and shaking the solution for 1 h. The solution was passed through a Whatman™ #1 filter (GE Healthcare Bio-Sciences, Pittsburg, PA, USA) and the extract frozen. A second subsample ($t + 1$) was placed inside a plastic cup, sealed, and allowed to incubate in the dark at room temperature for an average of 18 d (range: 14–21) before extraction. Percent soil moisture was measured gravimetrically from a separate 5 g subsample of t and $t + 1$ samples by oven-drying at 60° for a minimum of 48 h. We extracted inorganic-N in all extracts following Forster (1995) for NH_4^+ and Doane and Horwath (2003) for NO_3^-. Inorganic-N was then measured with a Shimadzu™ spectrophotometer (Shimadzu Scientific Instruments, Columbia, Maryland, USA) set at 650 nm for ammonium (NH_4^+) and 540 nm for nitrate (NO_3^-). NH_4^+ and NO_3^- concentrations were blank-corrected and expressed on a dry-weight basis as μg (NH_4^+ or NO_3^-)/g dry weight of soil. Inorganic-N pool sizes were determined from concentrations of NH_4^+ and NO_3^- at time t. Net N-mineralized was calculated as $[(NH^+_{4\,t+1} + NO^-_{3\,t+1}) - (NH^+_{4\,t} + NO^-_{3\,t})]$/number of incubation days. Percent nitrification was calculated as net nitrification/net N-mineralized, where net nitrification = $(NO^-_{3\,t+1} - NO^-_{3\,t})$/number of incubation days (Robertson et al. 1999).

For C, N, and δ^{15}N determination, soils were passed through a 2 mm mesh sieve, dried at 40–50 °C, and ball-milled. Oven-dried plant material was ground with a Wiley Mini-Mill™ (Thomas Scientific, Swedesboro, New Jersey, USA) through a 40 mesh sieve. Subsamples of dried and ground plant leaves and soil were then analyzed at the University California – Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL™ elemental analyzer interfaced to a PDZ Europa 20-20™ (Sercon Ltd, Cheshire, UK) isotope ratio mass spectrometer. Natural abundances of δ^{15}N in soils and plant tissues can be used to interpret broadly integrated N-cycling and N-sources (Nadelhoffer et al. 1996, Robinson 2001), and concentrated fecal and volatilized urine inputs often manifest into enriched soil $\delta^{15}N$ (Frank and Evans 1997).

Statistical analyses

We constructed mixed linear models to determine how our measures of ecosystem structure and plant and soil nitrogen varied along the island chronosequence of herbivory history, and relative to *Rangifer* spatial use intensity within islands. The island with nominal history (Kagalaska, ~0 yr) was set as the reference level for the chronosequence effect, and total number of pellet groups within transects ($\log_e$) indexed spatial use intensity (hereafter "spatial use"). Transect was treated as the random effect to account for correlation among plots within transects. Additional covariates comprising habitat type, elevation ($\log_e$), slope, northern aspect (cosine), and eastern aspect (sine) (Roberts 1986) were included in all models to consistently account for landscape-level variation in plant communities and edaphic conditions that can influence interactions between herbivory and ecosystem processes. Hence, we fit the same global main effects model for all response variables to test island and spatial use effects while accounting for all covariates, rather than constructing sets of competing models comprised of different combinations of covariates. However, we evaluated potential nonadditive effects of spatial use on all response variables by using log-likelihood ratio tests (Pinheiro and Bates 2000) to first compare fit of global models with spatial use treated as either a linear or quadratic effect. Nearly all tests supported the linear spatial use effect (see Results), so we then asked if linear effects varied consistently among islands by comparing the fit of global models with an island by spatial use interaction vs. main effects only models. Log-likelihood ratio tested models were fitted with maximum likelihood estimation, while final models were fitted with restricted maximum likelihood estimation (Pinheiro and Bates 2000) for reporting of effects. All final models were fit with the lme4 package (Bates et al. 2012), and F and P values using Satterthwaite approximated degrees of freedom were calculated with the lmerTest package (Kuznetsova et al. 2013) for program R (R-Core-Team 2014). To describe the island effect while accounting for all covariate effects at their mean level, we present model-based least squares means and confidence intervals calculated by lmerTest and back-transformed where necessary. In the rare instances when final models included interactions between island and spatial use, we report least squares means derived from island-specific slope coefficients. Heteroscedastic response variables, which included all biomass estimates, shrub mat depth, and soil inorganic-N pool sizes were $\log_e$ transformed. The model for shrub-mat depth was constrained to shrub habitats because extensive shrub-mats were typically absent in meadow habitats.

We summarized variation among ecosystem processes along the island chronosequence with nonmetric multidimensional scaling in Program PC-Ord (McCune and Grace 2002). We only included plots where biomass and cover of plant functional types and plant–soil nitrogen were measured (n = 253), and only included foliar-N measurements for *Calamagrostis* and *Carex* because *Anemone* was not encountered in all plots. We limited cover estimates of *Rangifer* forage to *Cladonia.* Because ecosystem processes measurements had different units, we converted all variables to "zero-mean unit length" by first subtracting the mean value of a given response from each value and then divided each now centered value by the standard deviation of a given response (Peck 2010). We excluded seven plots that were identified (SD >2.5) as strong outliers.

Given the lack of physical controls (e.g., exclosures) and spatial replication (e.g., multiple islands per treatment) in our study, we recognize that unidentified variation unrelated to *Rangifer* use (e.g., age of soil parent material) could confound our estimates of *Rangifer* spatial and temporal effects. However, our random sampling approach encompassed a similarly wide range of edaphic and topographic variation within islands to be reasonably accounted for by our statistical models, and large-scale soil classifications are identical among islands.

RESULTS

We sampled 27, 93, and 21 transects on islands with nominal, intermediate, and

Table 1. Number of plots sampled for ecosystem structure and soil nitrogen within heath and meadow habitats across islands in the Aleutian archipelago of Alaska enduring nominal (Kagalaska ~0 yr), intermediate (Adak~50 yr), and extensive (Atka~100 yr) history of herbivory.

	Kagalaska (~0 yr)		Adak (~50 yr)		Atka (~100 yr)	
Measurement	Heath	Meadow	Heath	Meadow	Heath	Meadow
Ecosystem structure	56	79	164	301	35	70
Soil nitrogen	16	29	48	101	17	46

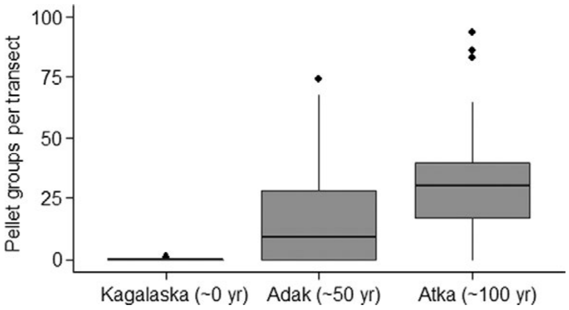

Fig. 2. Boxplots describing the number of fecal pellet groups detected along 400 m transects on islands in the Aleutian archipelago of Alaska enduring nominal (Kagalaska, ~0 yr), intermediate (Adak, ~50 yr), and extensive (Atka, ~100 yr) history of introduced *Rangifer* herbivory.

extensive history of herbivory, respectively. Within transects, a total of 705 and 257 plots were measured for ecosystem structure and soil nitrogen, respectively, across islands and habitat types (Table 1). Frequencies for *Rangifer* pellet groups detected along transects corroborated presumed *Rangifer* use across the island chronosequence (Fig. 2). Only one pellet group was detected across all nominal history transects. The median number of pellet groups was higher on extensive than intermediate history transects, although upper and lower quartiles overlapped.

Ecosystem structure

All measures of biomass and horizontal cover for plant functional types varied significantly along the chronosequence, whereby graminoid biomass increased ($F = 4.6$, $P = 0.01$), and dwarf-shrub biomass, shrub-mat depth, and total lichen cover decreased ($F \geq 7.5$, $P \leq 0.0008$) on islands with grazed histories (Fig. 3). Specifically, higher graminoid biomass was associated with intermediate and extensive histories compared to nominal history, whereas lower dwarf-shrub biomass was associated with extensive compared to intermediate and nominal history. Depth of the shrub-mat declined incrementally with history, and total lichen cover was dramatically reduced at both intermediate and extensive histories. Forb biomass decreased on the island with intermediate histories ($F = 3.1$, $P = 0.05$), and lower moss cover was associated with intermediate compared to nominal and extensive histories ($F = 14.8$, $P < 0.0001$).

Variation in functional type biomass and cover with spatial use (as indexed by pellet group counts) within islands was mostly opposite of among islands, whereby biomass of graminoids and forbs and depth of the shrub-mat negatively correlated with increasing spatial use intensity (Table 2). Biomass of dwarf-shrubs followed a marginally significant ($\chi^2 = 3.2$, $P = 0.07$) negative quadratic relation with spatial use where biomass was lower at intermediate and higher at low and high use. In contrast, total lichen and moss cover was invariant to variation in spatial use. Effects of *Rangifer* spatial use were similar across the chronosequence for all response variables (island*spatial use: $\chi^2 \leq 3.3$, $P \geq 0.2$) and all other quadratic models were insignificant ($\chi^2 \leq 1.0$, $P \geq 0.3$).

In contrast to responses among plant functional types, variation in horizontal cover of *Rangifer* forage taxa was not strongly related to the chronosequence, yet some interesting patterns emerged (Fig. 4). Within graminoid functional types, cover of grasses and sedges did not differ significantly among islands ($F \leq 1.1$, $P \geq 0.3$), although there was a trend of higher sedge and low-

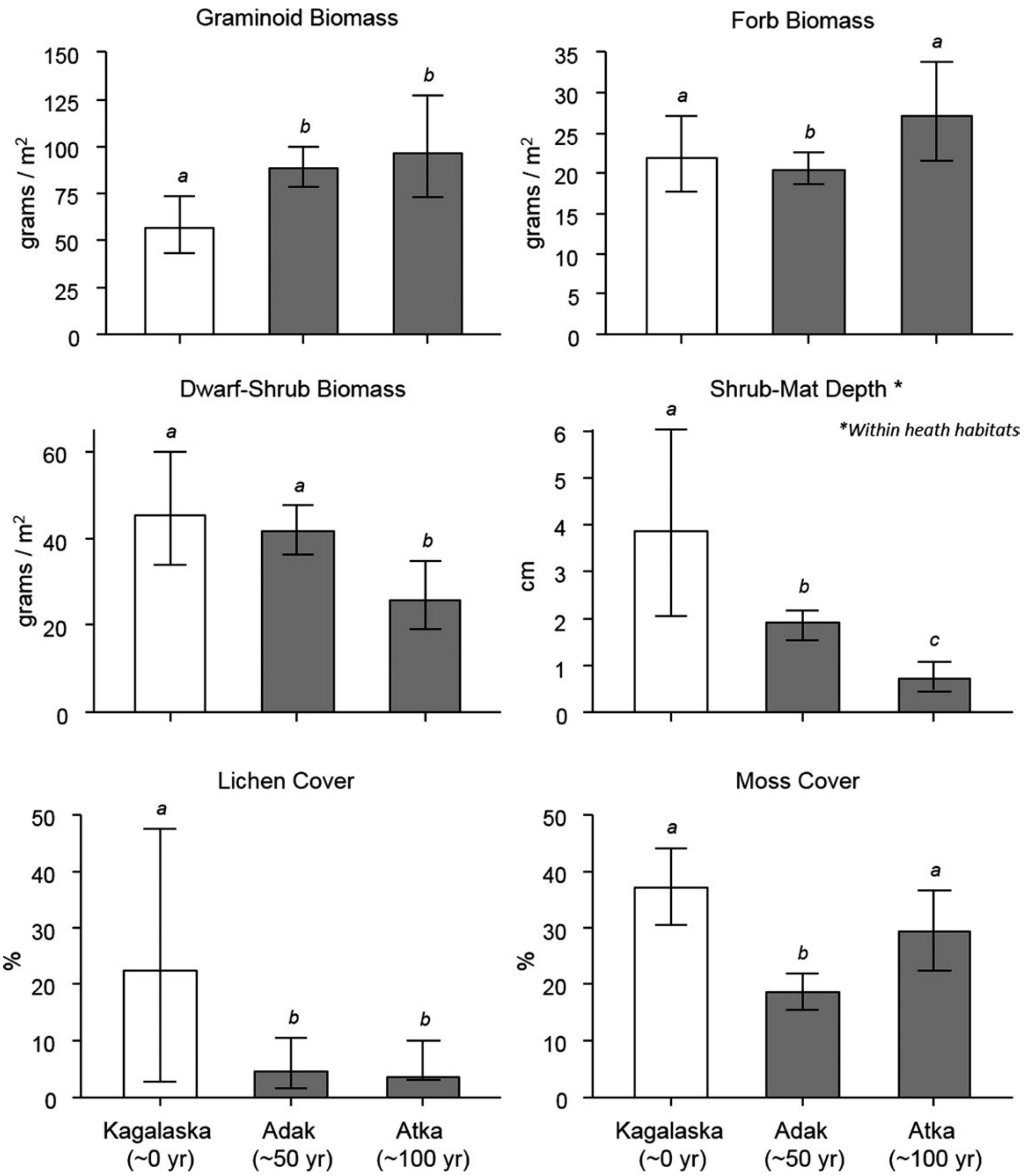

Fig. 3. Model-based least-squares means and 95% confidence intervals for measurements of plant functional-type biomass (or cover) and dwarf shrub mat depth on islands in the Aleutian archipelago of Alaska enduring nominal (Kagalaska, ~0 yr), intermediate (Adak, ~50 yr), and extensive (Atka, ~100 yr) history of introduced *Rangifer* herbivory. Islands sharing the same letter above error bars do not differ significantly.

er grass cover on the islands with intermediate and extensive histories. Cover of evergreen and deciduous dwarf-shrubs decreased significantly ($F \geq 3.7$, $P \leq 0.03$), with lower cover of all taxa associated with extensive compared with intermediate and nominal history. The clearest pattern occurred where nominal history had cover of *Cladonia* lichens nearly five times higher than intermediate and extensive history ($F = 21.0$, $P < 0.0001$). Cover of non-*Cladonia* lichens (<3%)

Table 2. Coefficients† describing linear and quadratic effects of *Rangifer* spatial use intensity (indexed by pellet group counts along 400 m transects) on measures of ecosystem structure on islands in the Aleutian archipelago of Alaska enduring nominal, intermediate, and extensive history of herbivory.

			Spatial use intensity					
			Pellet group count (log)			Pellet group count ^{2} (log)		
Measure	Functional type or taxa	Effect direction†	Coefficient	*t*	*P*	Coefficient	*t*	*P*
Biomass (log)	Graminoid	−	−0.08	−2.6	0.01	ns	ns	ns
	Forb	−	−0.07	−2.7	0.01	ns	ns	ns
	Dwarf shrub	U	−0.19	−2.2	0.03	0.4	1.8	0.08
Depth (log)	Dwarf shrub mat	−	−0.14	−2.3	0.03	ns	ns	ns
% Horizontal cover`	Lichen (all)	ns	0.22	0.6	0.5	ns	ns	ns
	Cladonia lichen	ns	−0.2	−0.4	0.7	ns	ns	ns
	Non-*Cladonia* lichen	ns	0.2	1.3	0.2	ns	ns	ns
	Moss	ns	−0.16	−0.2	0.8	ns	ns	ns
	Grass (all)	ns	−1.1	−0.9	0.4	ns	ns	ns
	Sedge (all)	ns	1.2	1.1	0.2	ns	ns	ns
	Anemone	−	−1.7	−3.7	0.0004	ns	ns	ns
	Plantago	+	1.5	1.9	0.06	ns	ns	ns
	Evergreen dwarf shrub	ns	1.7	1.7	0.1	ns	ns	ns
	Deciduous dwarf shrub	U	−8.9	4.8	<0.0001	2.6	4.9	<0.0001

† Models accounted for fixed environmental (island, habitat, topography) and random (transect) effects.

‡ Negative linear (−), positive linear (+), negative quadratic (U), not significant (ns).

was markedly lower than *Cladonia* cover and did not differ significantly along the chronosequence ($F = 1.2$, $P = 0.3$).

Variation in spatial use within islands had no significant effect on cover of grasses, sedges, evergreen dwarf-shrubs, *Cladonia* lichens, or *non-Cladonia* lichens (Table 2). Cover of deciduous shrubs followed a negative quadratic relation with spatial use similar to the pattern for dwarf-shrub biomass ($\chi^2 = 14.8$, $P = 0.0001$). All other quadratic models of spatial use intensity were insignificant ($\chi^2 \leq 1.0$, $P \geq 0.3$).

Soil nitrogen

Longer history of herbivory negatively impacted most measures of soil nitrogen and physical properties along the island chronosequence (Fig. 5). Initial pool sizes of total inorganic-N, NH_4^+, NO_3^-, total soil-N, and soil moisture declined incrementally with grazing history ($F \geq 32.3$, $P \leq 0.0001$). Ammonium was the dominate form of inorganic-N, comprising an average of 93–95% (SD: 2–5%) of the inorganic-N pool. Average rates of % nitrification were low (<25%) along the chronosequence, but higher nitrification was associated with nominal compared to extensive history. Nitrogen mineralization was roughly 10 times higher with nominal history compared to intermediate and extensive history where the majority of inorganic-N was immobilized by soil microbes ($F = 4.0$, $P = 0.04$). Striking differences in soil δ^{15}N values potentially indicating different nitrogen sources were also evident among islands ($F = 11.2$, $P = 0.0001$), whereby nominal and intermediate history was associated with positive values (and confidence intervals not overlapping zero) while extensive history was associated with δ^{15}N depleted negative values. In contrast to patterns for all other soil measures, C:N ratios varied nonlinearly among islands ($F \geq 4.8$, $P \leq 0.01$), whereby intermediate history was associated with higher C:N ratios compared nominal and extensive histories that did not differ from each other.

As was the case for measures of ecosystem structure, variation in spatial use seemed to oppose historical effects along the chronosequence for some, but not all, measures of soil-N and physical properties (Table 3). Spatial use

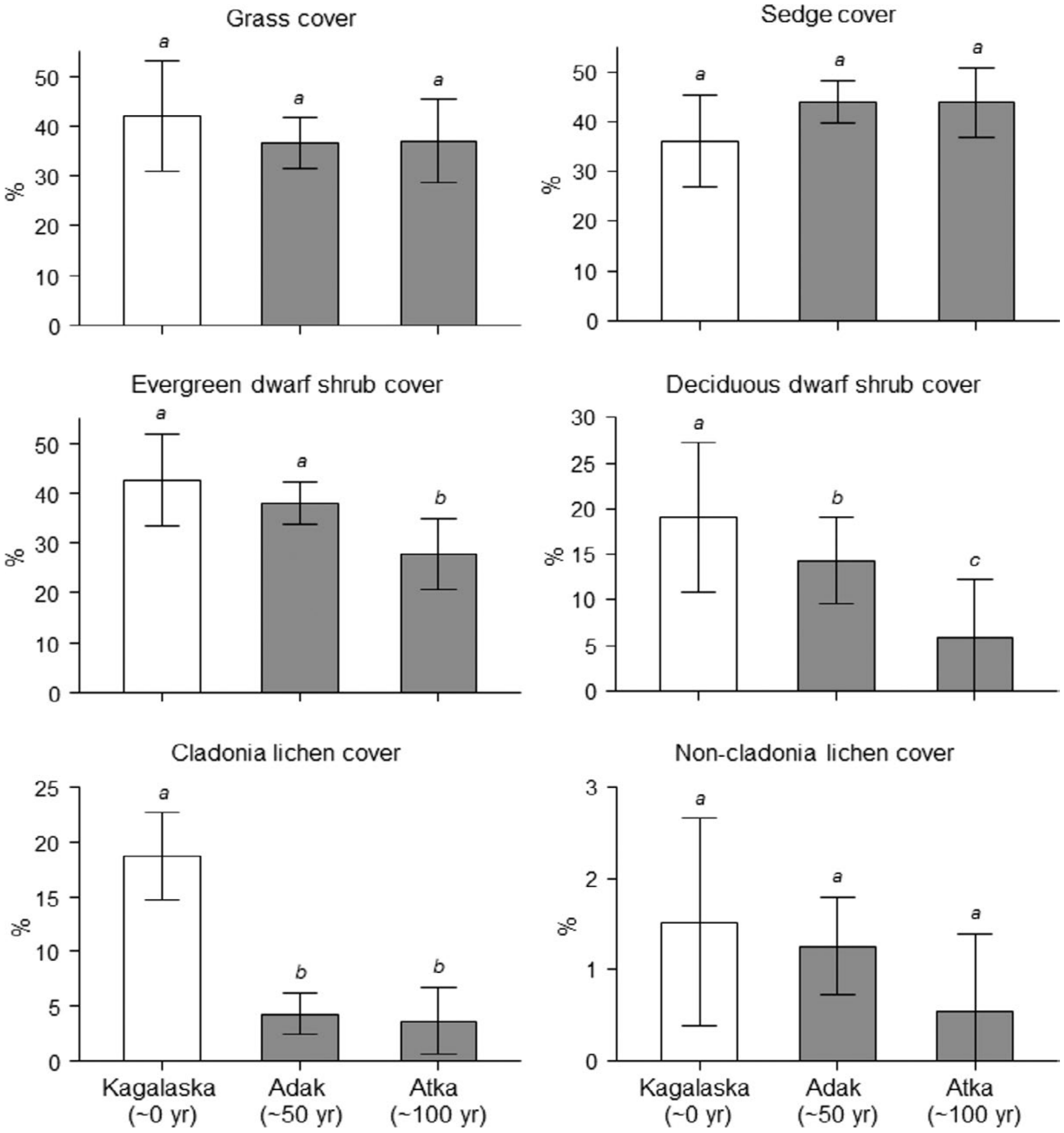

Fig. 4. Model-based least squares means and 95% confidence intervals for percent horizontal cover of *Rangifer* forage types on islands in the Aleutian archipelago of Alaska enduring nominal (Kagalaska, ~0 yr), intermediate (Adak, ~50 yr), and extensive (Atka, ~100 yr) history of introduced *Rangifer* herbivory. Islands sharing the same letter above error bars do not differ significantly.

intensity was positively correlated with all measures of initial inorganic-N pool size, total soil-N, and soil moisture. This was opposite of the grazing history pattern among islands. However, N-mineralization, % nitrification, δ^{15}N, and C:N were unaffected by spatial use intensity. Effects of spatial use intensity were similar across the chronosequence ($\chi^2 \leq 5.8$, $P \geq 0.06$), and all quadratic models of spatial use intensity were insignificant ($\chi^2 \leq 1.8$, $P \geq 0.1$).

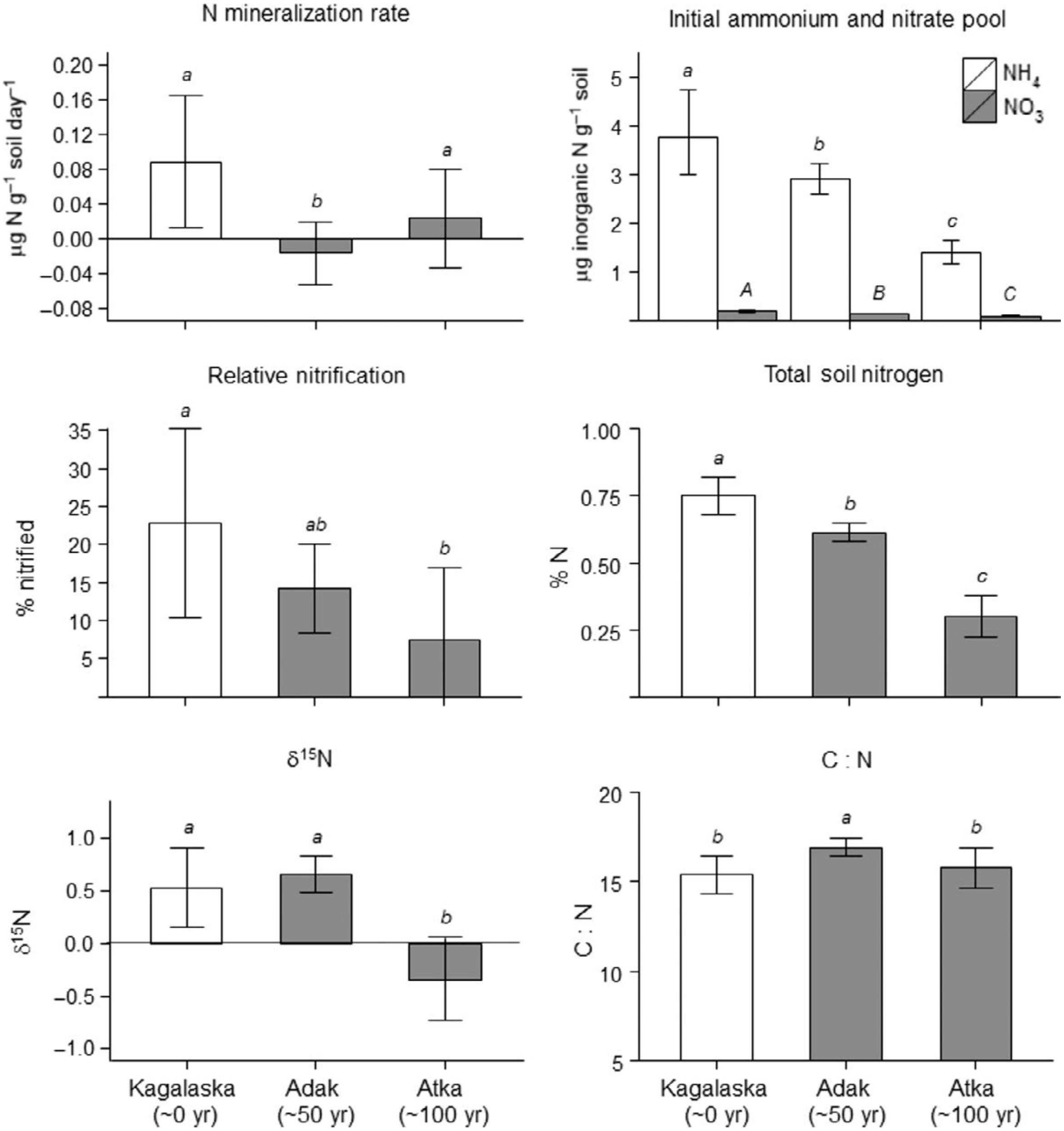

Fig. 5. Model-based least squares means and 95% confidence intervals for measures of soil nitrogen and physical soil properties on islands in the Aleutian archipelago of Alaska enduring nominal (Kagalaska, ~0 yr), intermediate (Adak, ~50 yr), and extensive (Atka, ~100 yr) history of introduced *Rangifer* herbivory. Means for islands sharing the same letter above error bars do not differ significantly.

Foliar nitrogen

As with soil δ^{15}N, variation in δ^{15}N in *Carex* and *Calamagrostis* along the chronosequence indicated potentially different sources of nitrogen (Fig. 6). Values of δ^{15}N in *Carex* followed a strong incremental depletion along the chronosequence ($F = 12.6$, $P < 0.0001$), and depleted values of δ^{15}N in *Calamagrostis* were associated with intermediate (but not extensive) history ($F = 8.3$, $P = 0.0003$). *Anemone* δ^{15}N did not

Table 3. Coefficients† describing linear effects of *Rangifer* spatial use intensity (indexed by pellet group counts along 400 m transects) on measures of soil nitrogen and soil physical properties on islands in the Aleutian archipelago of Alaska enduring nominal, intermediate, and extensive history of herbivory.

	Spatial use intensity			
		Pellet group count (log)		
Measure	Effect direction‡	Coefficient	*t*	*P*
N-mineralization rate	ns	−0.01	−1.4	0.15
Total inorganic–N initial pool size (log)	+	0.05	2.1	0.04
NH_4^+ initial pool size (log)	+	0.04	1.9	0.07
NO_3^- initial pool size (log)	+	0.06	3.8	0.0002
Relative nitrification (%)	ns	−0.46	−0.4	0.7
$\delta^{15}N$	ns	−0.05	−1.1	0.3
Total N (%)	+	0.0007	1.9	0.06
C:N	ns	−0.15	−1.2	0.2
$\delta^{13}C$	−	−0.06	1.9	0.06
Soil moisture (%)	+	1.76	3.7	0.005

†Models accounted for fixed environmental (island, habitat, topography) and random (transect) effects, all quadratic models were insignificant.

‡Negative linear (−), positive linear (+), negative quadratic (U), not significant (ns).

differ among islands (F = 1.3, P = 0.3). In contrast, %N generally increased along the chronosequence, which was opposite of the pattern for soil-N. Percent N in *Calamagrostis* increased incrementally along the chronosequence (F = 7.5, P = 0.0007), and higher %N in *Carex* and *Anemone* was associated with extensive history compared to nominal and intermediate history ($F \geq 12.9$, $P \leq 0.0001$). Patterns of foliar C:N followed an identical parallel pattern ($F \geq 8.6$, $P \leq 0.005$).

Variation in spatial use primarily influenced foliar nitrogen measurements in *Calamagrostis*. In addition, spatial use by island interactions occurred for some measurements in *Calamagrostis* and *Carex* ($\chi^2 \leq 7.5$, $P \geq 0.02$) (Table 4). For *Calamagrostis*, values of $\delta^{15}N$ became more depleted as spatial use intensified among all island histories, while %N and C:N positively and negatively correlated with spatial use intensity, respectively, at extensive history. C:N in *Carex* followed a similar pattern, which decreased as spatial use increased at extensive history. *Carex* $\delta^{15}N$, %N, and all measures for *Anemone* were not influenced by variation in spatial use.

Ordination of ecosystem processes

The positioning of plots in the NMS ordination space, which explained 78% of variation among ecosystem processes, indicated strongly divergent patterns associated with unmanaged *Rangifer* grazing for ~100 yr, and more overlapping patterns associated with an intermediate history of grazing, recent population irruption, and subsequent management intensity (Fig. 7). With the exception of three plots, extensive and nominal history plots completely segregated from each other in the ordination space, but were overlapped by intermediate history plots. Moreover, positioning of plot-centroids further indicated sequential differences in ecosystem processes along the chronosequence. Extensive history plots aligned with the upper right quadrant of the ordination space, which associated most strongly with the following processes: drier and $\delta^{15}N$ depleted soils with lower NH_4^+ pools; *Calamagrostis* with lower C:N; $\delta^{15}N$ depleted *Carex*; fewer forbs, dwarf-shrubs, and *Cladonia* lichens; and compacted dwarf-shrub mats. Nominal history plots aligned more broadly with the lower end of Axis 2, whereas intermediate history plots aligned more variably along both axes. Interestingly, variation in graminoid biomass did not drive axis loadings (R^2 < 0.08), and *Rangifer* spatial use was not correlated strongly ($R^2 \leq 0.1$) with either axis.

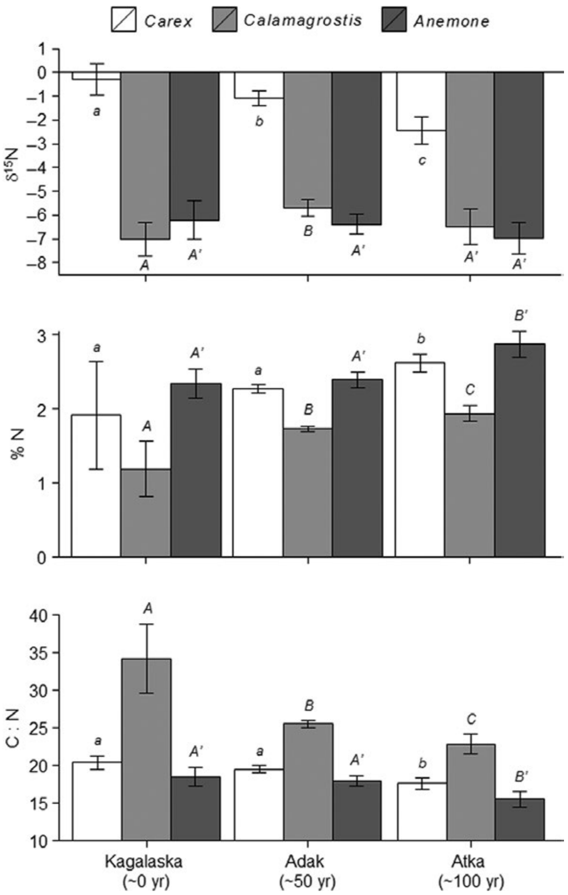

Fig. 6. Model-based least squares means and 95% confidence intervals for foliar nitrogen and carbon in common sedges (*Carex*), grasses (*Calamagrostis*), and forbs (*Anemone*) growing on islands in the Aleutian archipelago of Alaska enduring nominal (Kagalaska, ~0 yr), intermediate (Adak, ~50 yr), and extensive (Atka, ~100 yr) history of introduced *Rangifer* herbivory. Taxa-specific means for islands sharing the same lowercase or uppercase letter and prime symbol above error bars do not differ significantly.

DISCUSSION

Ecosystem structure and influences of history and spatial use

Inter-island (i.e., chronosequence) comparisons in our study measured historical impacts of grazing on vegetation communities, while associations with spatial use within each island measured the impact of current-summer herbivory in communities shaped by historical differences in grazing. Changes in plant community structure along the chronosequence largely followed an accelerating pattern, whereby graminoids appeared to fill the niche space afforded by the overall reduction of dwarf-shrubs, mosses, and lichens on grazed islands. These results are in accordance with long-term patterns observed on the arctic mainland (van der Wal 2006, Olofsson et al. 2009) and insular (Klein 1968, 1987, Leader-Williams 1988, Ouellet et al. 1994) tundra. Kitti et al. (2009) also described a similar inverse relation between shrub (*Salix*) and graminoid (*Eriophorum*) biomass after 50 yr of grazing pressure in mesic subarctic tundra. Long-term *Rangifer* grazing may also have a stimulatory effect on forage quality in maritime tundra given that foliar-N concentrations generally increased (and C:N decreased) along the chronosequence yet were mostly invariant to spatial use intensity. Graminoids and forbs often respond to defoliation by drawing on belowground stores to reallocate N aboveground (McNaughton 1979), and higher foliar-N in response to simulated clipping and actual grazing has been observed in many tundra systems (Ouellet et al. 1994, Post and Klein 1996, Olofsson and Oksanen 2002, Olofsson et al. 2004, van der Wal et al. 2004).

Within grazed islands, however, areas with a higher index of spatial use had less biomass of graminoids and forbs. This pattern conforms to predictions from herbivore optimization theory (McNaughton 1979, 1983, Hobbs 1996), whereby graminoids respond positively to low–moderate grazing intensity via compensatory growth and positive feedbacks with soil fertility, but then decline at higher levels of grazing intensity when plant growth cannot compensate for increased tissue-loss. Thus, while the long-term product of grazing appears to facilitate an overall increase in graminoid biomass, areas of high summer grazing pressure add a strong component of spatial heterogeneity within islands. Different response to herbivory pressure between grasses and sedges also adds further complexity to the historical and spatial pattern for graminoids. Though not statistically significant, higher sedge cover was measured on the islands with intermediate and extensive grazing histories and the trend with spatial use was positive. Sedges in our study also had higher levels of foliar nitrogen than grasses.

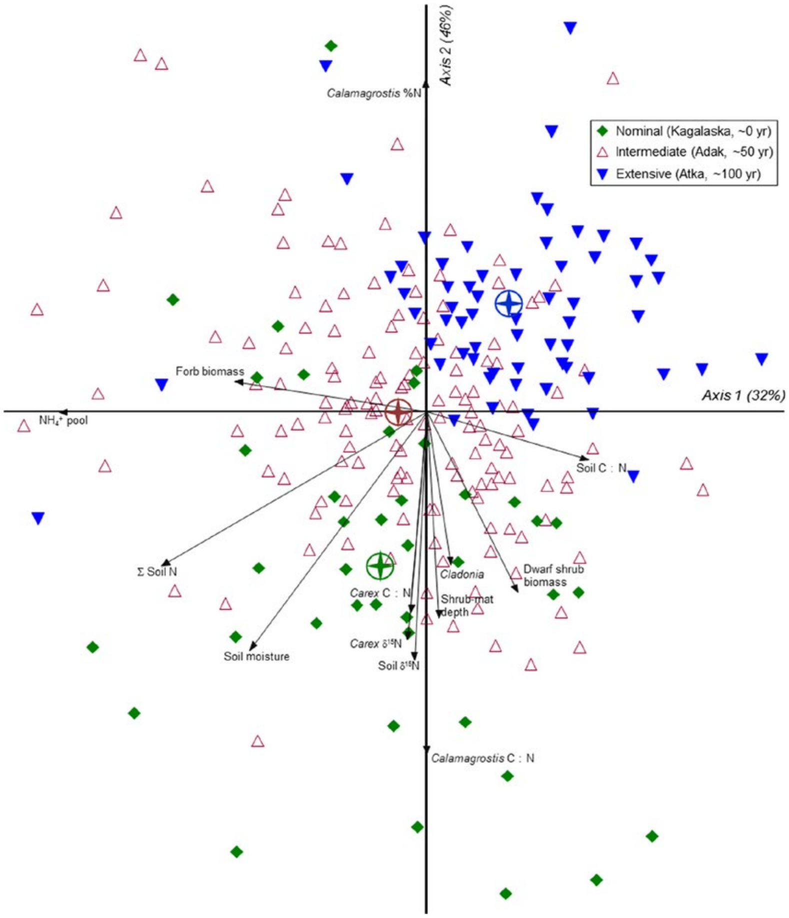

Fig. 7. Nonmetric multidimensional scaling ordination describing 78% of the variation in ecosystem processes within plots sampled for both plant and soil measurements along a chronosequence of islands in the Aleutian archipelago of Alaska enduring nominal (Kagalaska, ~0 yr), intermediate (Adak, ~50 yr), and extensive (Atka, ~100 yr) history of herbivory from introduced *Rangifer*. Vectors (arrows) represent the association and correlative strength ($r^2 > 0.2$) of dominant ecosystem processes along axes. Circular cross-hair symbols indicate centroids for each island.

Sedges are herbivory tolerant, and extensive grazing both temporally and spatially has been associated with increased sedge biomass (Klein 1987, Brathen et al. 2007, Kitti et al. 2009), and concomitant decreases in grasses (Klein 1990, Brathen et al. 2007).

Graminoids can respond positively to grazing due to increases in soil temperature stemming from reduced structural components of the dwarf-shrub community. While we did not measure soil temperature adequately to partition effects of temperature vs. available light, reduced leaf biomass of allelopathic evergreens like *Empetrum* and increased light penetration through thinner shrub-mats may be a more important physical mechanism for stimulating graminoid production than soil temperature in the milder climate of the Aleutians. Decreasing depth of the dwarf-shrub mat along the chronosequence and the positive relation with spatial use supports this contention. Brathen et al. (2010) also demonstrated how *Rangifer* trampling and defecation can negatively impact *Empetrum* leading to increases in graminoids and forbs.

Inter-island comparisons of functional types less-tolerant to herbivory further illustrated long-terms impacts to vegetation communities and

Table 4. Coefficients† describing linear effects of *Rangifer* spatial use intensity (indexed by pellet group counts along 400 m transects) on measures of foliar nitrogen and carbon in common sedges (*Carex*), grasses (*Calamagrostis*), and forbs (*Anemone*) growing on islands in the Aleutian archipelago of Alaska enduring nominal, intermediate, and extensive history of herbivory.

		Spatial use intensity			
			Pellet group count (log)		
Taxa	Measure‡	Effect direction§	Coefficient	t	P
Calamagrostis	δ^{15}N	−	−0.4	−3.6	0.004
	%N (intermediate)	ns	ns	ns	ns
	%N (extensive)	+	0.0002	2.9	0.004
	C:N (intermediate)	ns	ns	ns	ns
	C:N (extensive)	−	−0.4	3.3	0.001
Carex	δ^{15}N	ns	ns	ns	ns
	%N	ns	ns	ns	ns
	C:N (intermediate)	ns	ns	ns	ns
	C:N (extensive)	−	−0.2	−2.0	0.05
Anemone	δ^{15}N	ns	ns	ns	ns
	%N	ns	ns	ns	ns
	C:N	ns	ns	ns	ns

† Models accounted for fixed environmental (island, habitat, topography) and random (transect) effects, all quadratic models were insignificant.

‡ Island-specific models were fitted to estimate spatial use effect when significant interactions occurred.

§ Negative linear (−), positive linear (+), negative quadratic (U), not significant (ns).

subsequent shifts in available *Rangifer* forage, particularly in winter. Reductions of deciduous dwarf-shrub cover along the chronosequence indicated high palatability but relatively low tolerance to repeated browsing (Post and Pedersen 2008, Olofsson et al. 2009). While reductions in evergreen dwarf-shrub cover were likely influenced by trampling, this taxon can also comprise a significant proportion of winter diets (Klein 1990). Similar cover of non-*Cladonia* lichens among islands further illustrated strong forage preference for *Cladonia* lichens that could not withstand years of herbivory on a spatially constrained island. Notably, the remaining biomass of *Cladonia* on both grazed islands was highly fragmented in comparison to the robust mats we observed on the nominal history island. Moreover, the lack of a correlation between lichen cover and spatial use was not surprising given that it can take more than 30 yr for *Cladonia* to recover from overgrazing (Klein and Shulski 2009), so lichens may be rapidly depleted even in of areas of low grazing pressure on islands. These results, in conjunction with higher graminoid biomass on both grazed islands, support the hypothesis that *Rangifer* introduced to the islands without a strong arctic influence rely heavily on residual graminoid biomass after lichens mats and herbivory-intolerant forage become depleted as a source of usable energy during winter when protein demands are low (Klein 1968, 1991, Leader-Williams 1988, Mysterud 2006, Gross et al. 2010).

Long-term herbivory alters nitrogen cycling

In our study, lower rates of N-mineralization and nitrification combined with low inorganic- and total N pool sizes provide reasonable evidence that 50 and 100 yr of *Rangifer* grazing decelerates N-cycling and lowers soil fertility, while the effect of summer grazing intensity was weaker over the short term. Yet, we expected accelerating patterns for measures of soil nitrogen given the overall increases in graminoid biomass and foliar-N and concomitant decreases in shrub biomass along the chronosequence, whereas the inverse relation between spatial use and graminoids and forbs suggested low measures of soil nitrogen should be detected in areas of high use.

Weak or opposing linkages between above and belowground processes are not uncommon among studies of *Rangifer*-tundra interactions. While Olofsson et al. (2004) suggested that effects of continued grazing should drive higher rates of N-cycling along long-term scales of ecological time, Virtanen et al. (2008) described how increases in graminoids related to *Rangifer* grazing did not cascade belowground to strongly alter biomass of soil microbes and fauna that drive N-mineralization. Sorensen et al. (2008) found that repeated grazing was associated with decreased N-mineralization and plant-N uptake despite having no effect on plant abundance. Linkages between aboveground and belowground process in tundra ecosystems can also be weakened by high amounts of soil organic matter that decompose slowly, which then buffer belowground processes against changes to the quality and quantity of aboveground litter inputs (Stark et al. 2008). Increased N-availability from grazing can stimulate microbial respiration and enzyme activity necessary to accelerate decomposition of soil organic matter, yet Stark and Väisänen (2014) found microbial activity did not vary with grazing intensity or timing after plant communities shifted from dwarf-shrubs to graminoids. Thus, while decomposition rates in the maritime tundra of the Aleutians are faster than those experienced in arctic tundra (Ricca 2013), high levels of organic matter in soils and existing herbivore-driven shifts in vegetation may help explain opposing above and belowground responses in our study.

High inputs of "premineralized" *Rangifer* nitrogenous waste was a central process that led to our un-met prediction of higher soil-N pools and mineralization rates on grazed islands. Lower soil-N pools may have been due to N-loss, yet strikingly depleted δ^{15}N values in soils with extensive history did not match expected patterns derived from either N-loss from the system via leaching or denitrification, or high fecal inputs (Frank and Evans 1997). Consumption of foliage with δ^{15}N depleted by herbivory and subsequent excretion could also drive a feedback driving δ^{15}N depleted soil (Kielland and Bryant 1998). In our study, *Carex* comprised over 25% of summer diets in *Rangifer* on Atka based on fecal analyses (M.A. Ricca, *unpublished data*), and intensive grazing can reduce root biomass (Stark et al. 2003) that may have contributed to depleted foliar δ^{15}N in *Carex* from Atka. Hence, an extensive history of *Rangifer* herbivory may have resulted in *Carex* with shallower roots yielding δ^{15}N depleted leaves (and associated *Rangifer* nitrogenous waste) that contribute to δ^{15}N depleted soil. Finally, availability of organic-N and mycorrhizal associations, which can be important components of N-cycling in arctic tundra (Chapin et al. 1993, Nadelhoffer et al. 1996, Michelsen et al. 1998, Hobbie et al. 2000), may have been altered by grazing history. While not measured in our or other studies in the Aleutians, many of the ericaceous genera common to maritime tundra (e.g., *Salix, Vaccinium, Empetrum*) have strong ecto-mycorrhizal associations in mainland tundra ecosystems (Schulze et al. 1994, Nadelhoffer et al. 1996). Utilization of isotopically light organic-N in litter derived from plants with ecto-mycorrhizal associations has also been demonstrated for mainland tundra flora (Nadelhoffer et al. 1996). How grazing may have contributed to observed variability in nitrogen cycling our study is an intriguing question deserving of further study in the Aleutians.

Rangifer-induced ecosystem state

Hysteresis is a fundamental principle of alternative state theory, whereby a perturbation reverses ecosystem feedbacks and the resulting alternate state cannot easily be restored by simply reducing or removing the perturbation (Scheffer et al. 2001, Suding et al. 2004, Standish et al. 2014). Alternate states are capable of existence in terrestrial ecosystems across the Aleutian archipelago. In particular, decimation of nesting seabird populations by introduced foxes eliminated marine-derived-N in seabird guano that converted fox-infested islands away from fertile grasslands and into nutrient-poor heaths, with no recovery back to the fertile condition even after 20–80 yr post-fox removal (Croll et al. 2005, Maron et al. 2006).

A different type of alternative state in the Aleutians may have been created by at least 30 generations of largely unmanaged *Rangifer* grazing on Atka (extensive history), whereby aboveground processes largely followed an accelerated pattern but belowground processes tended to decelerate. Furthermore, a linear pattern of *Rangifer* impacts over time was quite evident in our NMS ordination that illustrated strongly divergent processes between extensive and nominal history, which were then overlapped by intermediate history processes. Increases in graminoid biomass likely facilitate persistence of island *Rangifer* but do not necessarily increase carrying capacity (sensu Olofsson et al. 2004, van der Wal 2006) owing to concomitant reduction in soil fertility with increasing grazing history. Hence, these findings are more in line with predictions of the exploitation ecosystems hypothesis (Oksanen and Oksanen 2000) and all four stages of the Riney–Caughley model. More variable and overlapping conditions on the intermediate history island of Adak appear to correlate with the more recent population irruption (Ricca et al. 2014). Lastly, the recent detection of caribou (albeit few) on the nominal history island of Kagalaska (Ricca et al. 2012) prohibited treatment as a true caribou-free control. Yet, most ecosystem processes on Kagalaska differed significantly from those on more heavily grazed islands, and total N and δ^{15}N in Kagalaska soils were similar to soils in other ungrazed islands in the Aleutians not receiving seabird nutrient subsidies (Maron et al. 2006). We conclude that caribou emigrating from Adak have had relatively little impact on Kagalaska ecosystem processes to date.

Though politically complex, management plans have been proposed for the eradication of caribou from Adak (USFWS and ADFG 1994), and the presence of nonnative *Rangifer* on federal refuge lands is of continued concern for resource managers charged with "protecting and restoring natural biodiversity of the Aleutian Islands" (USFWS 2013). Hence, a final question relates to the resilience of maritime tundra after dramatic reductions or removal of *Rangifer*. Subsequent to the exclusion of *Rangifer* on arctic islands, forbs and deciduous shrubs generally recovered quickly, graminoids either increased or declined, and mosses overtook space previously occupied by extremely slow-growing *Cladonia* lichens (Klein 1987, Leader-Williams 1988, Henry and Gunn 1991). However, slow ecosystem recovery following removal of introduced foxes (Maron et al. 2006) suggests low resilience from disturbances that influence nitrogen cycling in the Aleutians, such as long-term *Rangifer* grazing described in this study. Hence, it is difficult to predict precisely how ecosystem structure would respond to large culls or removal of *Rangifer,* and how subsequent changes to vegetation would cascade to affect belowground ecosystem function in the climatically milder maritime tundra of the Aleutians.

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