Predator-rodent-plant interactions along a coast-inland gradient in Fennoscandian tundra

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ABSTRACT

Spatial variation in the strength of trophic cascades in arctic tundra has been related to flows of subsidies across ecosystem boundaries. Here, we ask whether the relative strength of rodent-plant interactions would change from coastal tundra, where predators have access to marine subsidies, to non-subsidized inland tundra areas of northern Fennoscandia. We present a detailed evaluation of predator-rodent-vegetation interactions along a coast-inland gradient, during the 2011 rodent outbreak and the two following decline years, by using direct assessments of rodent impacts and tracing of marine-derived nutrients in the food web. Among predators, only parasitic jaegers *Stercorarius parasiticus* and red foxes *Vulpes vulpes* seemed to be subsidized by marine resources, showing higher breeding densities and activity near the coast. Contrary to this pattern, the availability of marine resources did not support higher breeding densities of the main rodent predator, the long-tailed jaeger *S. longicaudus*, since they relied on terrestrial prey while breeding, regardless of the distance to the sea. Near the coast, no evidence was found for lower rodent population growth rates in summer or weaker rodent grazing impacts. Instead, we documented pronounced damages caused by lemmings and voles on bryophytes and vascular plants, especially dwarf shrubs (e.g., *Vaccinum myrtillus*) all along the coast-inland gradient. Taken together, our results did not support the hypothesis that marine subsidies would trigger a trophic cascade in coastal tundra areas of northern Fennoscandia during a major rodent outbreak. Comparative observational and experimental studies at large spatial scales in various arctic regions are absolutely necessary for a better understanding of factors causing regional variations in the functioning of arctic food webs.

KEY WORD exclosure, herbivore, lemming, marine subsidies, population regulation, predator-prey interactions, trophic cascade, vole

INTRODUCTION

Predicting the impacts of future climate-driven environmental changes at northern latitudes requires an understanding of the mechanisms affecting spatial and temporal variations in plant biomass and production. Microtine rodents are key components in many arctic ecosystems as they represent the main trophic link between vegetation and predators (e.g., Batzli et al. 1980, Ims and Fuglei 2005). In unproductive tundra ecosystems of Fennoscandia (Virtanen 1997, 2000, Aunapuu et al. 2008, Olofsson et al. 2009, 2012, 2014, Hoset et al. 2014), Siberia (Tikhomirnov 1959, Chernyavski 2002) and Alaska (Batzli et al. 1980, Johnson et al. 2011), the large amplitude cycles of rodent populations have triggered dramatic annual changes in plant biomass, leading to periodic overexploitation of winter forage and to large-scale grazing impacts during outbreak years (Olofsson et al. 2012), and substantial changes in plant community compositions (Johnson et al. 2011; Olofsson et al. 2014). The intensity of rodent herbivory on tundra vegetation is also expected to vary in space due to landscape heterogeneity in the composition of plant, rodent and predator communities. For example, weak rodent impacts on arctic vegetation have been documented in areas where predation forces were strongest, probably caused by three-level trophic cascades (Aunapuu et al. 2008; Bilodeau et al. 2014; Hoset et al. 2014).

Identifying the factors causing variation in the strength of trophic cascades across ecosystems has received much attention from experimental and theoretical ecology (e.g., Borer et al. 2005, Marczak et al. 2007, Leroux and Loreau 2008). One important determinant of community regulation and ecosystem functioning is the spatial flow of energy, material and organisms (i.e. allochthonous inputs or spatial subsidies) among adjacent systems (Polis and Hurd 1996, Loreau and Holt 2004). Recent works conducted in the Canadian Arctic have acknowledged the potential important role of allochthonous inputs in the functioning of unproductive tundra ecosystems and the dynamics of arctic terrestrial consumers (Gauthier et al. 2011, Tarroux et al. 2012, Giroux et al. 2012, Legagneux et al. 2012). In various parts of the Arctic, several (semi-)generalist predators breeding in the tundra can benefit from allochthonous resources, either by feeding in the adjacent marine environment (on, e.g., carrions, seabirds, fish, marine invertebrates; Roth 2003, Killengreen et al. 2011), on migrating birds (e.g., geese; Giroux et al. 2012), or on anthropogenic food sources that occur nearby (i.e. food waste from sewage; Julien et al. 2014). Such subsidies can produce a direct numerical response in recipient predator populations by improving their breeding performance to a level that would not be sustained by autochthonous prey only, as has been documented for arctic foxes, *Alopex lagopus* (Roth 2003, Tarroux et al. 2012), red foxes, *Vulpes vulpes* (Zabel and Taggart 1989) and long-tailed jaegers, *Stercorarius longicaudus* (De Korte and Wattel 1988, Julien et al. 2014). Other works have further hypothesized that subsidized predators may, in some cases, suppress in situ prey (Polis and Hurd 1996, Polis et al. 1996) in a manner that is similar to apparent competition (Holt 1994). However, the cascading effects of allochthonous subsidies on the dynamics of arctic rodent populations and the biomass of tundra plants remain to be experimentally demonstrated.

Despite a large number of studies investigating rodent-plant interactions in Fennoscandian tundra, little is known about the potential role of spatial flows of marine inputs on tundra community regulation in this region. Along the northern coasts off Scandinavia, the ocean-land interface forms a large coastal ecotone where exchanges of nutrients and materials between the relatively high productive marine Arctic environment (Slagstad et al. 2011) and the low productive terrestrial tundra occur. Here, we investigated whether trophic cascades mediated by marine-derived resources can occur in coastal areas of Fennoscandian tundra. More specifically, we ask whether the relative strength of rodent-plant interactions, largely documented as strong in Fennoscandian inland tundra, changes along a coast-inland gradient. In this arctic region, rodent predators, such as red foxes and jaegers, have access to an ice-free shoreline throughout the year with relatively more stable resource availability compared to cyclic (or highly fluctuating) rodent abundance, and to seabirds and waders nesting on littoral cliffs and the shore during summer (e.g., Andersson 1971, Killengreen et al. 2011). As coastal areas contain prey from both the terrestrial and marine biomes, we hypothesize that such ecotones would support higher numbers of predators, compared to inland tundra areas without coastal access, as predicted by the “marine subsidies hypothesis” of Polis and Hurd (1996). Subsidized predators could also take advantage of peak rodent densities for reproduction. If the numerical responses of predators are strong enough to influence rodent populations and plant biomass, the summer growth rates of rodent populations should be lower near the coast, and the cascading impacts of predation should mitigate the impacts of rodents on vegetation. On the other hand, in the absence of top-down controls mediated by marine resources, rodent population growth rates should remain high during rodent peak summers in both coastal and inland tundra areas, and their impacts on vegetation should be uniformly large, regardless of the distance to the sea.

To test these hypotheses, we present a detailed evaluation of predator-rodent-vegetation interactions in three study areas scattered along a coast-inland gradient in subarctic Fennoscandian tundra, during the 2011 rodent outbreak and the two following years of decline. We conducted parallel surveys on the breeding numbers, activity and predation rates of avian and mammalian predators, the abundance and summer growth rates of rodent populations, and used direct assessments of rodent grazing impact, as well as tracing of marine-derived nutrients.

MATERIAL AND METHODS

STUDY SITES AND THEIR VEGETATION

This study was conducted in three areas along a coast-inland gradient in western Finnmark, Norway (Fig. 1), on plateau-type tundra above the willow, *Salix* spp., scrubland limit (at 380 m.a.s.l. on the coast, at 520 m.a.s.l. in the inland). At the maritime end of the gradient, we chose an area (hereafter COAST; total area = 22.4 km^2) stretching from the shores of Altafjord in Skillefjordnes (Skirvinjárga; 77º86'N, 05º86'E), where the tundra plateau reaches the immediate vicinity of the coast, to a mountain range (8 km inland) that stands above the altitudinal limit of continuous vegetation (highest point 699 m.a.s.l.). The intermediate area (hereafter INTERM; total area = 34.1 km^2), stretched from this mountain range to 9 km further inland. At the inland end of the gradient, we selected the highland plateau of Joatka Research Area (69º45' N, 23º55' E; hereafter INLAND; total area = 29.0 km^2), located 35 km from the nearest sea shore, and where previous studies indicate that such highlands are characterized by food limited-rodent populations (e.g., Moen et al. 1993, Aunapuu et al. 2008, Olofsson et al. 2014). The coast of Altafjord is an important summer breeding area for seabirds, especially kittiwakes (Frantzen et al. 1991), and the ice-free coast provides access to marine invertebrates, fish, waders and other marine-derived food resources that may drift onshore.

In all three study areas, habitats suitable for rodents were mainly characterized by meadow and heath snow-beds, and bilberry (*Vaccinium myrtillus*) heathlands. Meadow snow-beds were dominated by grasses (e.g., *Antoxantnum odoratum*, *Festuca rubra*, *Phleum alpinum* and *Poa alpina*) and forbs (e.g., *Ranunculus acris* and *Leontodon autumnalis*). Patchy bryophyte cover (primarily *Sanionia uncinata*) existed in gaps where the cover of grasses and forbs was open. Lichens were uncommon. Heath snow-beds were dominated by mosses (mainly *Dicranum fuscescens*, *Kiaeria* spp. and *Polytrichum* spp.), lichens (mainly *Cladonia* spp., *Cetraria* spp. and *Stereocaulon* spp.), trailing dwarf willows (*Salix herbacea*), evergreen woody and semi-woody plants (mainly *Diphasiastrum alpinum* and *Vaccinium vitis-idaea*) and drought resistant sedges (mainly *Carex bigelowii* and *C. lachenalii*). Meadow snow-beds prevailed on the coastal peninsula, while heath snow-beds prevailed in the inland. Bilberry heathlands occurred in all study areas, but covered a larger fraction of the tundra habitats near the coast.

HERBIVORE AND PREDATOR COMMUNITIES

The rodent community of northern Norwegian tundra highlands consists of Norwegian lemmings (*Lemmus lemmus*), which eat graminoids and mosses (Soininen et al. 2013a), grey-sided voles (*Myodes rufocanus*), which eat dwarf shrubs, preferentially bilberry twigs, and field voles (*Microtus agrestis*), which eat graminoids and forbs (Soininen et al. 2013b). During summers of high densities, woody shrubs, especially evergreen ericoids, are also impacted by lemmings, even though barely eaten (Dahlgren et al. 2009, Soininen et al. 2013a, Olofsson et al. 2014). Lemming dynamics are characterized by irregular, short-lived outbreaks (the previous ones occurred in 2007, 1988 and 1978), interspaced by periods with very low numbers. Grey-sided voles, which prevail at low altitudes (Henttonen and Viitala 1982) and had fluctuated at low numbers in tundra highlands during 1977-2014, have regular cycles with a dominating period of five years (Ekerholm et al. 2001; LO, KH, unpublished data).

The predator community of these highland areas is mainly composed of long-tailed jaegers, parasitic jaegers (*Stercorarius parasiticus*) and red foxes, which are known to prey on voles and lemmings, and alternatively on marine-derived resources such as fish, marine arthropods, seabirds and carrion washed ashore (e.g., Andersson 1976, Andersson and Götmark 1980, De Korte and Wattel 1988, Killengreen et al. 2011). Arctic foxes are uncommon in our study areas. Small mustelids, i.e. stoats (*Mustela erminea*) and least weasels (*M. nivalis*), only occasionally exploit areas above the willow scrubland limit in inland Fennoscandian tundra (Oksanen et al. 1992). Birds of prey (i.e. rough-legged hawks *Buteo lagopus,* merlins *Falco columbarius,* short-eared owls *Asio flammeus,* hawk owls *Surnia ulula*) breed in western Finnmark (Frantzen et al. 1991) but are rarely found in the highlands of our study areas.

MONITORING PREDATOR NUMBERS AND BREEDING SUCCESS

During the 2011 rodent peak year and the two following years of decline, we investigated whether the vicinity of the marine environment allowed jaegers to reach higher breeding numbers and success than would be possible in the absence of marine resources. Monitoring breeding birds started mid-June when most jaegers had settled in a territory and built a nest. A group of three to five persons systematically searched the three study areas by walking along parallel lines 100 m apart. The openness of their breeding habitat and their conspicuous aggressive behavior around the nest (Andersson 1976) allowed for an exhaustive mapping of all jaeger nests during the three summers. Once a nest had been discovered, its fate was checked twice later in the season, covering both the incubation and chick-rearing periods. Breeding densities were calculated by excluding habitats that were unsuitable for them to breed (i.e. lakes, mountain ranges ≥ 600 m of elevation, barren and rocky habitats, forests). Rough-legged hawks were breeding outside the margins of our study areas (i.e. below the willow scrubland limit) in summer 2011. They occurred in low densities (~0.03 pair/km^2) and were rarely observed hunting in our study areas (i.e. in highland tundra). Their impact on rodents was thus considered to be low compared to the predation mortality imposed by jaegers.

The winter activity of the four mammalian predators (i.e. red foxes, arctic foxes, least weasels, stoats) was monitored by means of snow-tracking, which provides comparable indices of abundance among study areas and years (e.g., Pulliainen 1981). Winter activity was monitored in the three study areas by skiing along a transect line late December 2011, late March-early April 2012 and early January 2013. Transect length was 7.46 km, 8.77 km and 3.44 km in COAST, INTERM and INLAND, respectively. The direction and length of the skiing route were optimized to cover most habitat types and elevation ranges within each study area. COAST study site was divided in two sections: the first section ($\text{COAST}_{\text{Slope}}$) covered the coastal area from 40 m to 300 m of elevation and included patches of herb-rich scrublands and forest woodlands. The second section ($\text{COAST}_{\text{HighPlateau}}$) covered a tree-less plateau from 300 m to 480 m of elevation further inland. Snow-tracking was done only when conditions were optimal, i.e. after a fresh snowfall and when the weather was calm (not windy and not snowing), allowing us to separate fresh tracks from old ones and to maximize their detection. Each mammal track crossing transect lines was mapped and identified to species (for criteria, see Oksanen et al. 1992). An index of winter activity was calculated for each species by dividing the total number of tracks by the distance covered by ski (e.g., Pulliainen 1981).

Another index of stoat and weasel winter activity was obtained by searching systematically all study areas in spring 2012, after snowmelt, and recording both intact winter nests of rodents (mainly lemmings; voles prefer to winter in cavities) and those showing signs of predation by small mustelids (e.g., Gilg et al. 2006). The presence of fur, bones or mutilated bodies was taken as evidence for predation. Differences in the number of predated winter nests among areas were tested with Fisher exact tests for count data as some values were < 5. Differences were considered significant at $P < 0.017$, after a Bonferroni correction was applied due to pair-wise comparisons of the same dataset. Finally, footprint tracking tunnels (Pest Control Research, New Zealand) were used to assess the summer activity of small mustelids in all three study areas in 2012 and 2013 (tracking tunnels could not be used in summer 2011 due to extremely high rodent densities interfering with mustelid footprints in tunnels). At each study site, 30 permanent tracking stations (one tunnel per station) were distributed every 300 m along leading lines of most favored mustelid habitats, e.g., creeks, lakes, bushy vegetation, and monitored every five days at four consecutive occasions in August, when the activity of mustelids, especially young stoats, was the highest (Aunapuu 2004). Tracking papers were renewed when animal footprints were recorded. At each sampling occasion, each tunnel was scored for presence or absence of mustelid tracks and an overall index of summer activity for each area was calculated as the average number of occasions showing tracks at each tunnel. Differences in summer activity among areas were tested with non-parametric Kruskall-Wallis rank sum tests.

DIET OF JAEGERS AND IMPORTANCE OF MARINE RESOURCES

We quantified the relative importance of rodents and marine resources in the diet of both jaeger species during their breeding season by combining analyses of regurgitated pellets and stable isotopes. The analyses of stable isotopes in jaeger tissue also allowed tracing marine-derived nutrients along the coast-inland gradient, as previously done for red foxes and arctic foxes (e.g., Killengreen et al. 2011, Dalerum et al. 2012; see also Julien et al. 2014). Pellets were searched extensively within each jaeger territory, focusing on nest surroundings and mounds. All fresh pellets were dissected, prey items were identified and the frequency of occurrence of rodents and marine-derived resources (i.e. fish, marine invertebrates) was calculated. Rodents were identified to the genus level (*Myodes*, *Microtus*, *Lemmus*) based on morphological features of the jaws and skulls found in the pellets. We analyzed the ratios of naturally occurring stable isotopes in the feathers of jaeger chicks before fledging during the 2011 and 2012 summers, using stable-carbon ($^{13}C/^{12}C$ or $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$ or $\delta^{15}N$) isotope ratios, to estimate the relative proportions of each category of prey in the assimilated diet of the chicks (see Supplementary material Appendix 1 for additional technical details). Stable isotope composition of chick feathers reflected the diet of the chicks since feathers had started growing, and therefore reflected the prey hunted by the parents during the chick-rearing period. After initial preparation of the samples, isotopic measurements were performed at the Stable Isotope Laboratory of Environment Canada, Saskatoon, Canada. The assimilated dietary proportions in jaeger tissues were estimated with isotope mixing models implemented in the R package SIAR (Stable Isotope Analysis in R; Parnell and Jackson 2015). In order to account for the sensitivity of isotopic mixing models to discrimination factors used, sensitivity analyses were performed. They are presented in Supplementary material Appendix 1, along with additional methodological details on stable isotope analyses.

Since marine organisms are enriched in ^{15}N and ^{13}C, we predicted that if jaegers were foraging in the marine environment while breeding, their chicks would show higher $\delta^{15}N$ and $\delta^{13}C$ values, as compared to the birds that fed on terrestrial prey only. This conjecture was tested by performing linear mixed models with Gaussian distribution error and identity link (LMM), using the lme4 package in R 3.0.2, where log(Distance to the Sea) was included as a fixed factor, Chick Age as a covariate and Nest ID as a random factor to reduce pseudo-replication due to the sampling of two chicks of the same nest. The normality in residuals was checked from quantile–quantile plots and the heteroscedasticity with residual versus fitted plots. Finally, differences in mean $\delta^{15}N$ and $\delta^{13}C$ values between long-tailed (year 2011) and parasitic jaegers (years 2011 and 2012 pooled) were tested with non-parametric Mann-Whitney tests.

RODENT NUMBERS, SUMMER RODENT POPULATION GROWTH AND PREDATION RATE

To determine whether proximity to the sea influenced rodent population dynamics, indices of lemming and vole abundance were obtained in meadow snow-beds, heath snow-beds and bilberry heathlands by bi-annual snap-trapping with the small-quadrat method (Myllymäki et al. 1971) on 10 quadrats in COAST, 15 quadrats on INTERM and 15 quadrats on INLAND. Five replicates per habitat type (two habitats only in COAST due to the absence of heath snow-beds) were trapped in the spring and fall of years 2011, 2012 and 2013. Spring trapping occurred mid-June, soon after snowmelt, while fall trapping occurred mid-September before snow cover settled. Three snap-traps were placed at each corner of each 15 m x 15 m quadrat (trapping effort = 240 and 320 trap-nights at each site and session). Traps were baited with rye bread, checked the following day and deactivated the third day. The small quadrat method is particularly suitable for monitoring rodent population dynamics in tundra landscapes that show high habitat heterogeneity at a very small scale resulting to profound small scale variation in small rodent densities (Ekerholm et al. 2011, Aunapuu and Oksanen 2003) (refs). Indices of vole and lemming abundance were calculated as the total number of individuals trapped per 100 trap-nights, corrected for the relative cover of all three tundra habitat types in each study area (B. Johansen, unpublished data). We tested whether the abundance of lemmings and voles in fall 2011 varied between study areas with LMM, where Habitat Type was included as a random variable. Snap-trapping indices were log-transformed before the analyses. In addition, we calculated summer growth rates (λ) of vole and lemming populations as follows: $\lambda_{summer} = \log(N + 1)_{fall} - \log(N + 1)_{spring}$, where N is the total number of voles or lemmings trapped during a season in each study area. Finally, in order to allow comparison of rodent densities with other arctic regions, we performed simple linear regressions between a series of snap-trapping indices and density estimates obtained with live-trapping from 1997 to 2011 in the tundra highlands of JRA (i.e. our INLAND site). This allowed us to obtained estimates of vole and lemming density in COAST and INLAND, where only snap-trapping indices are available. Further details about density calculations are regression analyses are presented in Supplementary material Appendix 3.

Summer predation rates on rodents were obtained by estimating the number of voles and lemmings eaten daily by jaegers, the most abundant predators in our study areas, using direct observations at the nests and data from pellet analyses. Observations of foraging behavior covered the 24-h day period and were conducted from incubation (late June) to the end of the chick-rearing period (mid-July) by two persons, ~30 and 200 m from the nest, using binoculars and a telescope. These observations indicated that a pair of long-tailed (n = 3 nests; 72 hours) and parasitic (n = 2 nests; 60 hours) jaegers with two young could eat up to 8 rodents.day^{-1} during the 2011 rodent peak summer. In summer 2012, data indicated that a pair of long-tailed jaegers could eat up to 2 rodents.day^{-1} (n = 2 nests; 72 hours), whereas a pair of parasitic jaegers usually ate only 1 rodent.day^{-1} (n = 2 nests; 48 hours). In summer 2013, long-tailed jaegers did not breed in any of our study areas, and due to the very low vole densities and absence of lemmings, no predation event by parasitic jaegers on rodents was observed (2 nests; 12 hours). The share of voles and lemmings taken daily was deducted from the analysis of pellets, which provided the average number of voles and lemmings occurring in one pellet (Supplementary material Appendix 2, Table A2a, b). Based on the breeding density of jaegers observed in the field during the chick-rearing period, when predation on rodents was the highest, we derived an estimate of the maximal number of voles and lemmings eaten per day and km^2 during summers 2011 and 2012 in each study area. Our estimates of the impact of jaeger predation are based on the highest daily consumption rates observed in the field and thus provide maximal estimates of their impact.

IMPACT OF RODENTS ON VEGETATION

The impact of rodents on vegetation was documented by three different methods. First, to assess the extent of damage caused by winter herbivory, we documented the proportion of above-ground vegetation that had been destroyed by rodents in 2011 and 2012, directly after snow melt, on the quadrats set up for rodent trapping. In each of the three study areas, five quadrats were monitored in meadow snow-beds and five in bilberry heathlands (the two habitat types which were present in each study area). We estimated rodent grazing impact by laying a tape along the diagonal of each quadrat (length of line: 15.9-42.7 m) and then calculated the proportion of impacted sections (i.e. sections where > 50 % of the ground was either scraped bare or covered by remnants of destroyed plants without live plants underneath the dead litter), after removing sections with unsuitable habitat (very wet habitat without vegetation or rocks with diameter > 10 cm). This method assessed the extent of damaging destructive grazing over the preceding winter but was insensitive to selective removal of preferred food items, such as bilberry twigs. We tested whether winter grazing impact varied among areas and years by performing a linear model with Gaussian distribution error and identity link (LM), where Year, Area, Habitat type and the interaction Year*Area were included as fixed factors.

Second, we estimated the intensity of the interaction between rodents and bilberry shoots over winter 2011-2012. In late June-early July 2011, we marked 20 bilberry shoots with freeze clips at each corner of 29 trapping quadrats (10 in COAST, 10 in INTERM, 9 in INLAND) in both meadow snow-beds and bilberry heathlands. In late June-early July 2012, after snowmelt, we calculated the total proportion of bilberry shoots that has been clipped by rodents during winter (other categories included dry, i.e. killed due unfavorable weather, and undamaged shoots). To test whether the proportion of bilberry shoots clipped by rodents varied among areas, we performed a LM where Area and Habitat were included as fixed factors, and the plot-level abundance of rodents in fall 2011 as a fixed covariate.

Third, the impact of rodent grazing on plant biomass was assessed by estimating the biomass of vascular plants and bryophytes between exclosures and open reference plots in the two extremities of our coast-inland gradient, i.e. COAST and INLAND. Lichens (present in INLAND only) were included in bryophyte samples but, since rodents do not eat lichens, lichen data will not be presented here. We established four clusters of five experimental plots in the prevailing highland tundra habitats of each area (i.e. meadow snow-beds on COAST, heath snow-beds in INLAND). Each cluster had one rodent-free exclosure in the center and four open control plots located two meters from it towards each of the four cardinal directions. Exclosures were constructed from mink cage net (mesh size: 1.27 x 1.27 mm; height: 50 cm, dug 10 cm in the soil; size of open plots: 50 cm x 50 cm; size of exclosures: 1 m x 1 m). None of the exclosures showed signs of vole or lemming impact the following spring. Clusters were set in late fall 2010 at INLAND and in early fall 2011 at COAST. In order to avoid bias due to differences in start year, the COAST clusters were established in areas where no sign of winter grazing were detected in summer and early fall 2011. Hence the vegetation of all exclosures had developed without visible rodent impact since the previous lemming outbreak in 2007-08. In August 2012, the above-ground parts of vascular plants from all experimental plots were harvested and sorted out by taxa.. In INLAND, bryophytes were harvested by taking 16 cores using a round corer with a diameter of 3 cm, placed along four lines (distances between subsequent lines and subsequent cores in the same line:10 cm), immediately after the harvesting of vascular plants. Bryophytes were also sorted out by taxa. Due to logistical constraints, the COAST cores were sampled in spring 2014, immediately after snow-melt; yet so that bryophytes on the coast had more time (fall 2012 and summer 2013) to recover before harvesting than bryophytes in the inland. Hence our estimates of rodent impact on bryophytes remain are especiallyconservative for the coast. All plant material was dried at 50°C for 48 hours and then weighed to obtain total biomass for vascular plants and bryophytes. Differences in rodent grazing on vascular plants and bryophytes over winter were tested by performing LMMs where Area, Treatment and their interaction were included as fixed factors. Cluster was included as a random factor in the analyses to account for the fact that each group of four open plots was directly compared to its relative exclosure. The response variable Biomass was log-transformed to meet the assumption of normality in the data.

RESULTS

PREDATOR NUMBERS, ACTIVITY AND BREEDING SUCCESS

During the 2011 rodent peak year (Fig. 2), breeding pairs of long-tailed jaegers occurred in higher densities compared to the two following rodent decline years (Table 1). Breeding densities and clutch sizes were substantially lower in summer 2012, while in summer 2013, long-tailed jaegers did not breed at all. In 2011 and 2012, the densities of long-tailed jaegers were similar in COAST and INLAND, but slightly higher in INTERM. On the other hand, parasitic jaegers never bred far from the shore (91% of nests < 4 km; n = 11); their breeding densities were constant among years, but fairly low (3-5 pairs; Table 1).

Snow-tracking during winter 2011-2012, a few months following the summer rodent outbreak, showed a gradual decrease in red fox activity from the coast to further inland (Table 2). Arctic foxes were also more active in the high plateau of COAST and in INTERM, although the number of tracks recorded was substantially lower than for red foxes. During winter 2012-2013, the activity of both fox species sharply dropped in all study sites, but remained slightly higher in INTERM. During both winters, the activity of small mustelids was highest in the slope section of COAST that included herb-rich scrublands and birch woodlands.

After the 2011-2012 rodent outbreak, the percentage of rodent winter nests depredated by small mustelids was the lowest in INLAND (2.4%, $N = 165$) compared to INTERM (11.0%, $N = 174$; Fisher exact test: odds-ratio = 0.16, 95% CI = [0.04-0.51] , $P < 0.0001$) and COAST (9.3%, $N = 199$, Fisher exact test: odds-ratio = 0.19, 95% CI = [0.05-0.59] , $P = 0.001$). There was no significant difference between INTERM and COAST (Fisher exact test: odds-ratio = 1.07, 95% CI = [0.52-2.21], $P = 0.86$). The summer mustelid activity was also lowest in INLAND, but differences among study areas were not statistically different (mean number of occasions with mustelid tracks per tunnel ± SD; August 2012, COAST: 0.08 ± 0.24, INTERM: 0.16 ± 0.48, INLAND: 0 ± 0, *P* = 0.28, Kruskall-Wallis rank sum test; August 2013, COAST: 0.04 ± 0.20, INTERM: 0.08 ± 0.36, INLAND: 0 ± 0SD, *P* = 0.78, Kruskall-Wallis rank sum test).

DIET OF JAEGERS AND IMPORTANCE OF MARINE RESOURCES

The chicks of long-tailed and parasitic jaegers showed different mean δ^{15}N and δ^{13}C ($U = 320$, Z = -4.71, $P < 0.001$) values with low variation between study areas. The feathers of parasitic jaeger chicks ($N = 10$) were enriched in both ^{15}N (mean ± SD $\delta^{15}\mathrm{N}_{\mathrm{parasitic}} = 12.94 \pm 0.84‰$; mean $\delta^{15}\mathrm{N}_{\mathrm{long\text{-}tailed}} = 5.08 \pm 0.64‰$) and ^{13}C (mean ± SD $\delta^{13}\mathrm{C}_{\mathrm{parasitic}} = -19.70 \pm 0.45‰$; mean $\delta^{13}\mathrm{C}_{\mathrm{long\text{-}tailed}} = -24.34 \pm 0.31‰$), as compared to those of long-tailed jaegers ($N = 32$), suggesting a larger importance of marine resources in the diet of parasitic jaeger chicks (see Supplementary material Appendix 1, Fig. A1). Mixing models on isotopic ratios of chick feathers revealed that the relative contribution of marine resources in the diet of long-tailed jaeger chicks was low in 2011 (0-3% in all sites; Fig. 3a, c). In addition, there was no effect of the distance to the sea on chick δ^{15}N ($\beta = -0.15$, $SE = 0.20$, $P = 0.46$) and δ^{13}C ($\beta = -0.04$, $SE = 0.04$, $P = 0.30$) values. Conversely, marine resources (including fish and marine invertebrates) accounted on average for 41% (95% CI = 29-54%) of the assimilated diet of parasitic jaeger chicks, when years 2011 and 2012 were pooled (Fig. 3d).

Stable isotope analyses revealed that rodents accounted for 30-32% of the assimilated diet of long-tailed jaeger chicks in all three study areas in summer 2011 (Fig. 3c). The analysis of pellets also showed a large consumption of rodents by adults (Fig. 3a), with an average minimum of 1.12 (0.05SD) individual rodents per pellet in 2011, and 1.17 (0.02SD) rodents per pellet in 2012 across all three sites. Parasitic jaegers also preyed on rodents during summers 2011 and 2012, but to a lesser extent than long-tailed jaegers: rodents accounted on average for 12% of the assimilated diet of the chicks (Fig. 3d), and the average minimal number of individual rodents found in pellets was

1.10 (0.30SD) and 1.00 (0.47SD) in 2011 and 2012, respectively. In 2013, when rodent abundance crashed to very low levels, rodents occurred in 11% of parasitic jaegers´ pellets (Fig. 3b).

RODENT NUMBERS, SUMMER RODENT POPULATION GROWTH AND PREDATION RATE

In all three study areas, rodent populations started to build up toward peak density in summer 2011, and crashed to substantially lower levels by the following summer (Fig. 2, 4). In fall 2011, vole populations reached higher numbers in COAST ($\beta = 0.017$, $SE = 0.004$, $P < 0.001$) and INTERM ($\beta = 0.010$, $SE = 0.003$, $P < 0.0015$) than in INLAND. Conversely, lemming numbers were lower in COAST ($\beta = -0.010$, $SE = 0.005$, $P = 0.07$) and INTERM ($\beta = -0.009$, $SE = 0.005$, $P = 0.046$) than in INLAND. Rodent numbers also varied among biotope types, with lower abundances in meadow (voles: $\beta = -0.013$, $SE = 0.003$, $P < 0.001$; lemmings: $\beta = -0.021$, $SE = 0.005$, $P < 0.001$) or heath (lemmings: $\beta = -0.011$, $SE = 0.005$, $P = 0.043$) snowbeds than in bilberry heaths (vole numbers did not differ between bilberry heaths and heath snowbeds: $\beta = 0.020$, $SE = 0.004$, $P = 0.64$).

Based on the linear regressions between snap-trapping and live-trapping indices (see Supplementary material Appendix 3 for methods), landscape-weighed densities of voles in fall 2011 (i.e. weighed over the relative cover of snow-beds and bilberry heaths in the landscape) were estimated to reach 3 800, 2 590 and 481 voles.km^{-2} in COAST, INTERM and INLAND, respectively. Landscape-weighed densities of voles in fall 2011 were estimated to reach an average of 211, 201 and 422 lemmings.km^{-2} in COAST, INTERM and INLAND, respectively. At the habitat scale (when indices are not weighed), vole density could reach 17 800 voles.km^{-2} in fall 2011 in the bilberry heaths of COAST, while lemming density could reach 1 191 lemmings.km^{-2} in fall 2011 in the meadow snow-beds of INLAND.

The summer population growth rate of voles and lemmings in 2011 was positive in all three areas, and highest in COAST (Fig. 4). In addition, whereas vole population growth rates sharply dropped to null values in both INLAND and INTERM in summer 2012, and in INLAND in summer 2013 (Fig. 4), they remained positive in COAST in both summers, and in INTERM in summer 2013 (Fig. 4). No lemmings were caught in any of the study areas in summers 2012 and 2013 (Fig. 2b).

During the chick-rearing period of summer 2011, long-tailed and parasitic jaegers ate a maximum of 2.2 voles and 1.5 lemmings.day^{-1}km^{-2} in INLAND, 3.3 voles and 1.0 lemmings.day^{-1}km^{-2} in INTERM and 3.4 voles and 1.5 lemmings.day^{-1}km^{-2} in COAST daily. In summer 2012, jaegers ate a maximum of 0.1 vole.day^{-1}km^{-2} in both COAST and INTERM (Supplementary material Appendix 2, Table A2b).

IMPACT OF RODENTS ON VEGETATION

Overall, the impact of rodent grazing measured along line transects was stronger in meadow snow-beds than in bilberry heathlands (β = 0.30, *SE* = 0.04, $P < 0.001$; Fig. 5a, b). While the impact recorded in summer 2011 was of similar magnitude in the three study areas, it increased in summer 2012, but only in a significant manner in COAST (β = 0.30, *SE* = 0.10, $P = 0.003$).

The proportion of bilberry shoots clipped by rodents did not vary along the coast-inland gradient (all *P* values > 0.48), but was nearly two times higher in meadow snow-beds (>70% impact), as compared to bilberry heathlands (β = 0.31, *SE* = 0.06, $P < 0.0001$; Fig. 5c). In addition, rodent abundance in fall 2011 positively affected rodent impact on bilberry shoots (β = 0.60, *SE* = 0.26, $P < 0.05$).

The exclosure experiment revealed significantly lower vascular plant (β = -0.63, *SE* = 0.26, $P = 0.025$) and bryophyte (β = -0.32, *SE* = 0.11, $P = 0.008$) dry biomasses in open plots than in rodent-free exclosures following the rodent outbreak (Fig. 6), regardless of the distance to the sea (vascular plants, Site*Treatment: $\beta = -0.17$, $SE = 0.37$, $P = 0.65$; bryophytes, Site*Treatment: $\beta = 0.08$, $SE = 0.16$, $P = 0.60$).

DISCUSSION

Using direct assessments of rodent impacts on plants and tracing of marine-derived nutrients, this study evaluates whether the relative strength of rodent-plant interactions would change along a coast-inland gradient of tundra landscapes. Our findings confirmed the results of previous studies in inland areas of western Finnmark and northern Swedish and Finnish Lapland showing that the inland high-plateau tundra areas of this region are characterized by strong rodent-plant interactions (Virtanen 1997, 2000, Olofsson et al. 2012, 2014). Our results also document higher overall predator numbers and predation rate by jaegers and mustelids near the coast during 2011-2013. However, we found no evidence that this additional predation pressure was sufficient to release the vegetation from rodent impacts near the coast. Instead, we documented large-scale rodent grazing impacts after the 2011 rodent outbreak, regardless of the distance to the sea, suggesting that marine-subsidies to predators did not cascade down to the plants in coastal tundra of northern Fennoscandia during a major rodent outbreak and the following winter.

Our results concerning predators are in accordance with the prediction based on the “marine subsidies hypothesis” of Polis and Hurd (1996), i.e. that arctic coastal ecotones can support larger numbers of predators than inland highland tundra areas. Similar patterns have been observed in coastal arid deserts, on islands and along rivers, where the subsidizing impact of aquatic resources declines steeply with increasing distance from the shoreline (e.g., Rose and Polis 1998, Hilderbrand et al. 1999, Power et al. 2004). The observed spatial variation in predator distribution and abundance along the coast-inland gradient can be related to the availability of extra resources (i.e. of marine origin) in the vicinity of the sea. Indeed, the reliability of parasitic jaegers on marine resources to breed contributed to the overall higher jaeger (both species combined) breeding densities documented near the coast during the three years of survey. Moreover, the gradual increase in winter fox activity from inland to coastal tundra areas during the winter following the 2011 rodent peak may indicate that, in coastal western Finnmark, red and arctic foxes utilize marine resources during winter as shown for red foxes in Alaska (Zabel & Taggart 1989), and for arctic foxes in Canadian Arctic (Roth et al. 2003, Tarroux et al. 2012), coastal Iceland (Dalerum et al. 2011) and Siberia (Bannikov 1969). Killengreen et al. (2011) even showed that marine-derived resources could account for up to 50% in the winter diet of coastal red fox populations in eastern Finnmark. Other alternative, but not mutually exclusive, hypotheses to explain the differences in predator numbers and activity between study areas can pertain to varying weather conditions, rodent species and landscape compositions between the two ends of the gradients, that could have affected, e.g., predator hunting success or movements. For example, during the winter 2011-2012 of rodent declining abundance, foxes might have tracked rodents where they were more easily accessible, i.e. at the coastal and intermediate study areas due to a thin snow cover (< 30 cm) allowing them to access lemmings by digging (TO and LO, unpublished data). Furthermore, lower jaeger breeding densities in our inland study site may be explained by poor hunting success in lemming-dominated tundra areas, such as the highlands of northern Fennoscandia during lemming peak summers (see also Andersson 1976 for lemming/vole abundance ratios in similar habitats). Indeed, long-tailed jaegers may be less successful in capturing Norwegian lemmings than voles due to their more efficient anti-predator behavior and aposematic coloration (Andersson 2015). Finally, the higher mustelid activity in the peninsula is more likely related to landscape features, such as leading lines or ecological corridors, i.e. creek valleys, connecting the highlands to forested areas (Fig. 1c), rather than exploitation of marine resources. Indeed, the little knowledge available on the diet composition of weasels and stoats in coastal arctic areas indicates that the relative contribution of marine resources is low (Feige et al. 2012). In addition, marine resources were certainly not exploited by mustelids in the intermediate area since the high elevated, steep and barren mountain range (600-

699 m) separating the inner and coastal parts of the peninsula probably precluded any movements by mustelids.

Despite higher predator numbers observed in the peninsula than further inland, the pressure imposed by predators did not seem reach a level that would release vegetation from rodent impacts in coastal areas after the outbreak. One possible explanation may be related to the behavior of predators, especially predators´ level of preference for autochthonous prey, which has been identified as a key factor determining the strength of a trophic cascade (Leroux and Loreau, 2008). The main rodent predator in our study areas in summer, the long-tailed jaeger, was only poorly utilizing marine resources when breeding near the coast, whereas autochthonous prey (e.g., rodents, insects, berries) were clearly preferred. The populations of long-tailed jaegers from our study sites followed the same breeding patterns described in inland Sweden (Andersson 1976), i.e. they have evolved a reproductive strategy which is strictly dependent on oscillating rodent abundance (see also Barraquand et al. 2014). Since adult fitness and chick survival are maximized by strong territorial behavior (Andersson 1971), and foraging at sea would leave the chicks undefended for long periods, the over-all reproductive strategy of long-tailed jaegers has selected against conducting such foraging trips even in areas where the sea is close enough to make such foraging trips energetically rewarding. Conversely, parasitic jaegers, when not colonial, often have small territories to defend (e.g., Andersson 1971) and have evolved to utilize marine resources for reproduction during low rodent years (Andersson and Götmark 1980). Nevertheless, parasitic jaegers did not apparently breed in sufficient numbers in our coastal study area to trigger strong predation controls on rodents during summer. It is important to note however that, in the absence of data on the functional responses of predators to varying rodent densities and on the relative fraction of rodent population taken daily by predators, our study does not allow quantifying the relative importance of summer predation on rodent population dynamics. In addition, studying the diet of mammalian predators would have shed light on the differential predation rates imposed on rodents across study sites. However, the uniformly strong strength of rodent-plant interactions in both coastal and inland tundra areas documented in the present study indicates that our conclusions remain robust.

Compared to its Canadian and Greenlandic counterparts, where predation plays a crucial role in the regulation of lemming populations during the snow-free period (Gilg et al. 2006, Therrien et al. 2014), the overall diversity of the marine-subsidized predator pool in Fennoscandian tundra is low, probably due to a combination of factors related to human persecution, climate change and evolutionary processes. Snowy owls (*Bubo scandiacus*), which feed in the Arctic sea during winter in Canada, i.e. on open-water patches where waterfowl aggregate (Therrien et al. 2011), are nowadays critically endangered in Fennoscandia (Potapov and Sale 2012). While arctic foxes are key predators in the Canadian and Greenlandic tundra (e.g., Roth 2003; Gilg et al. 2006), the Fennoscandian arctic fox population has remained at a critically small size for almost a century due to human persecution (Hersteinsson et al. 1989). In addition, intensive red fox culling campaigns to protect endangered populations of arctic foxes and lesser white-fronted geese (see e.g., Killengreen et al. 2011) have reduced red fox populations in some areas of Finnmark. It is also important to notice however that red foxes remain very abundant in Fennoscandia and strong rodent-plant interactions have already been documented in the high tundra plateaus before fox culling started (e.g., Virtanen 1997, 2000; Aunapuu et al. 2008). Breeding densities of rough-legged hawks that mainly subsist on small rodents have remained low for the past 40 years in northern Fennoscandia (see Terraube et al. 2014 for an example from Finnish Lapland, 60-100km from our study areas), in comparison to the Canadian arctic tundra, where the species is among the most abundant rodent predators in coastal tundra areas (Therrien et al. 2014). Finally, the distribution and abundance of jaeger species show some contrasting regional patterns. For example, Pomarine jaegers (*Stercorarius pomarinus*), which depend on marine resources during winter and abound in *Lemmus* habitats from Pomor (the arctic coast of European Russia) to the Canadian Arctic, are absent from

Fennoscandia (e.g., Ruffino and Oksanen 2014). Moreover, despite high densities of rodent prey, the breeding densities of long-tailed jaegers observed in northern Fennoscandia during outbreak summers (0.4-0.7 pairs.km^{2}, this study; 0.5-0.65 pairs.km^{2}, Andersson 1976) remained lower than in the Canadian (Bylot Island: 0.9-1.1 pairs.km^{-2}, Therrien et al. 2014; Lake Hazen, Ellesmere Island: ~0.8 pairs.km^{-2}, Maher 1970) and Greenlandic (NE Greenland: ~0.9 pairs.km^{-2}, Gilg et al. 2006) high Arctic. The hypothesis that avian predators in our study areas may have reached their carrying capacity during the rodent peak summer in 2011 can be rejected since neither suitable breeding habitat or food abundance was limiting for jaegers during that year (L. Ruffino, unpublished data). A more likely hypothesis can be related to increasing competitive interactions with parasitic jaegers (Maher 1974) towards lower arctic latitudes leading to fewer breeding opportunities for long-tailed jaegers in coastal Low Arctic. Surely, tracking the movements of migrating long-tailed jaegers (e.g., Sittler et al. 2010, Gilg et al. 2013) may give insights on how wintering conditions at lower latitudes affect breeding population sizes across the Arctic.

Regional differences in types and amount of allochthonous subsidies across the Arctic can account for variations in the strength of trophic cascades among regions (Leroux and Loreau 2008). The absence of cascading effects of marine-derived resources observed in our coastal tundra area of northern Fennoscandia might indeed result from relatively low inputs of subsidies into the tundra ecosystem. Greater seasonal inputs at the predator level may be experienced by Arctic areas with a coastal access to sea ice most of the year. In the high Arctic sector of Canada for example, arctic foxes can prey on seals or scavenge on carcasses left by polar bears and hunters until early July, when the sea ice melts (Tarroux et al. 2012). Regional variations in fish stocks may also affect their local availability for rodent predators, as well as the distribution of seabird colonies, which are both important food sources for red foxes and jaegers. Nevertheless, a comparative evaluation of the production and fluxes of marine subsidies across time and arctic regions, integrating measurements of nutrient and organism stocks, is still crucially needed to test this hypothesis.

Rodent grazing intensity was uniformly severe all along the coast-inland gradient, despite distinct rodent community compositions and diet preferences. While the bryophyte depletion observed in snow-beds during winter 2011-2012 can be attributed to lemmings (e.g., Soininen et al. 2013a, Hoset et al. 2014), grey-sided voles are probably responsible for most of the loss of deciduous woody plants during winter (e.g., Soininen et al. 2013b). However, in years of high rodent abundances, lemmings have been documented to eat a variety of diverse food items, such as evergreen and deciduous scrubs, forbs and graminoids (Soininen et al. 2013a), and have also been observed to strongly impact ericoid shoots by damaging (but not eating) plant materials standing on their way (pers. obs.). Such behavior may explain the extremely high proportion of clipped bilberry shoots observed in the tundra highlands of our inland study area, dominated by Norwegian lemmings. Interestingly, the grazing impact recorded along transect lines was higher near the coast after the outbreak. Winter conditions near the coast (little or no snow in early winter, and then rapid accumulation of snow under calm weather in January-March 2012; see eklima.org) might explain this pattern. The intensity of rodent grazing seemed also to vary with habitat types, with greater damage documented in snow-beds compared to heathlands. A likely explanation is that the deep snow layer accumulated in snow-beds during winter creates a soft layer of snow at the bottom, facilitating foraging by rodents on woody plants and mosses (e.g., Virtanen 1997). This highlights the importance of considering small-scale spatial variation in grazing impacts, as well as the heterogeneity of habitat structures within the landscape, when evaluating the impact over large spatial scales.

The high rodent densities documented in our study sites during summer 2011 were not exceptional in northern Fennoscandia since densities of similar magnitudes have already been observed in the past during combined lemming and vole peaks (see, e.g., Andersson 1976 for the 1972-1975 period, and Olofsson et al. 2012 for the 1998-2011 period). They are also in accordance with peak brown lemming densities documented in Alaska and Siberia (>10 000 rodents per km^2;

Batzli et al. 1980, Chernyavski 2002). These numbers contrast, however, with the low densities of rodents (i.e. collared and brown lemmings) documented during peak summers in the Canadian Arctic (< 200 individuals/km^2, Reid et al., 1997; < 250 individuals/km^2, Therrien et al. 2014) and in Greenland (< 1 500 individuals /km^2, Gilg et al. 2006), where summer predation mortality has been shown to exceed the maximal daily population growth rate of lemming populations. In these arctic regions, the winter impact of lemmings on plant biomass is invariably low, regardless of rodent abundance (Bilodeau et al. 2014). Beside predation intensity, other factors such as the diversity of the rodent guild, climate and landscape composition (e.g., spatial variation in production of herbaceous forage; Oksanen et al. 2013, and abundance realtionships between lemming habitats and unsuitable areas such as polar deserts, semi-deserts and glaciers; Walker et al. 2005) can explain the regional differences in rodent abundance and grazing intensity across the Arctic.

Our three-year parallel monitoring of predator-rodent-vegetation interactions along a coast-inland gradient did not support the hypothesis that marine subsidies would trigger a trophic cascade in coastal areas of Fennoscandian tundra, probably due to a low diversity and density of marine-subsidized predators. Further empirical evidence, including rodent consumption rates by predators, as well as numerical and functional responses of predators to varying densities of lemmings and voles, are still needed to better evaluate the role of predation on rodent population dynamics and test the generalities of our findings at the regional scale. Cross-ecosystem empirical research is also highly desirable in areas where marine subsidies are likely to be a key factor strengthening top-down controls of tundra systems. This is probably the case of some pristine areas of the High Arctic (e.g., Canada, Greenland) where the diversity and density of marine-subsidized predators is higher than in Fennoscandia and predators have access to an almost permanently frozen sea which provides additional resources (e.g., seal carrions to arctic foxes, waterfowl to snowy owls). More generally, the causes and consequences of spatial heterogeneity of rodent grazing impacts deserve a greater attention, as their understanding can help developing scenarios of plant biomass and production under climate change at both small (e.g., regional) and broad (e.g., circumpolar Arctic) spatial scales.

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TABLES

Table 1. Breeding densities (no. of pairs.km^{-2}) and breeding success of long-tailed and parasitic jaegers in 2011-2013 along a coast-inland gradient

	2011			2012			2013		
	COAST	INTERM	INLAND	COAST	INTERM	INLAND	COAST	INTERM	INLAND
Number of breeding pairs *S. longicaudus*	6	15	13	1	4	1	0	0	0
Number of breeding pairs *S. parasiticus*	4	1	0	3	0	0	3	0	0
Mean clutch size *S. longicaudus*	2	1.9	2	1	1.75	1.6	.	.	.
Mean clutch size *S. parasiticus*	2	1	.	2	.	.	1.33	.	.
Breeding density at laying*	0.40 (0.67)	0.74 (0.78)	0.54	0.07 (0.20)	0.20	0.04	(0.17)	.	.
Breeding density at chick rearing*	0.34 (0.64)	0.54 (0.54)	0.46	0 (0.13)	0.05	0	(0.17)	.	.

*Numbers outside brackets refer to breeding densities of long-tailed jaegers only, while numbers within brackets refer to breeding densities of both jaeger species.

Table 2. Mean index of winter activity (no. of tracks.km^{-1}) of foxes and small mustelids estimated by snow-tracking along a coast-inland gradient

	Early winter 2011-2012				Late winter 2011-2012				Early winter 2012-2013			
	V. vulpes	*A. lagopus*	*M. erminea*	*M. nivalis*	*V. vulpes*	*A. lagopus*	*M. erminea*	*M. nivalis*	*V. vulpes*	*A. lagopus*	*M. erminea*	*M. nivalis*
COAST$_{\text{(Slope)}}$	OBS*	/*	/*	OBS*	5.61	0	2.46	0	0	0	1.05	3.35
COAST$_{\text{(High plateau)}}$	/*	/*	/*	/*	2.5	0.18	0.53	0	0	0	0	0
INTERM	3.65	1.94	0	0.11	0	0.57	0	0	0.11	0	0	0
INLAND	0.78	0.26	0	0	0.52	0	0	0	0	0	0	0

* Due to unsuitable snow conditions in the coastal area of the peninsula, snow-tracking could not have been conducted in December 2011. However, some observations (OBS) of red fox (n = 2) and least weasel (n = 3) tracks were made in COAST between 75 m and 130 m of elevation.

FIGURE LEGEND

Figure 1. Map showing the three (a panel) study areas (COAST and INTERM: b panel; INLAND: c panel) scattered along a coast-inland gradient in western Finnmark, Norway.

Figure 2. Average weighed trapping index of voles (a) and lemmings (b), expressed as the number of individuals captured/100 trap-nights, in the three study areas from spring 2011 to fall 2013. Bars show standard errors. Indices have been weighed over the relative cover of each habitat type in the landscape (i.e. some habitats that are more favorable for rodents but cover a relatively small area could have shown a trapping success > 10%; for example, the combined trapping success for all rodents in bilberry heaths in INTERM during fall 2011 reached 52% (13% SD)).

Figure 3. Percentage of occurrence of rodents and marine-derived resources in adult pellets (a, b) and mean relative dietary proportions derived from isotopic mixing models (95% confidence intervals are shown; c, d) in long-tailed (a, c) and parasitic (b, d) jaegers. Sample sizes are indicated in brackets for each study site (COAST, INTERM, INLAND). Note that the full results of isotopic mixing models detailed for each prey category are described in Table A1.

Figure 4. Summer growth rates of lemming (LEM) and vole (VOL) populations in 2011-2013 along a coast-inland gradient.

Figure 5. Proportion of stretches that showed > 50% damage by rodents in early summer 2011 (reflecting grazing damage over winter 2010-2011) (a) and 2012 (reflecting grazing damage over winter 2011-2012) (b), and proportion of bilberry clipped by rodents from summer 2011 to summer 2012 (c). Bars show standard errors. Sample sizes were, for the damage survey (a), 5 quadrats in meadow snow-beds and 5 quadrats in bilberry heathlands in each of the three study areas, and for the bilberry survey (b), 10, 10 and 9 quadrats in COAST, INTERM and INLAND, respectively.

Figure 6. Average biomass of vascular plants and bryophytes in fenced and open snow-bed plots from COAST (a) and INLAND (b) documented following the 2011 rodent outbreak. Bars show standard errors. Sample sizes were four clusters of one fenced and four open plots in both study areas. The above-ground part of vascular plants was harvested in August 2012 in both areas. Bryophytes were harvested in August 2012 in INLAND and in spring 2014 in COAST.

Figure 1

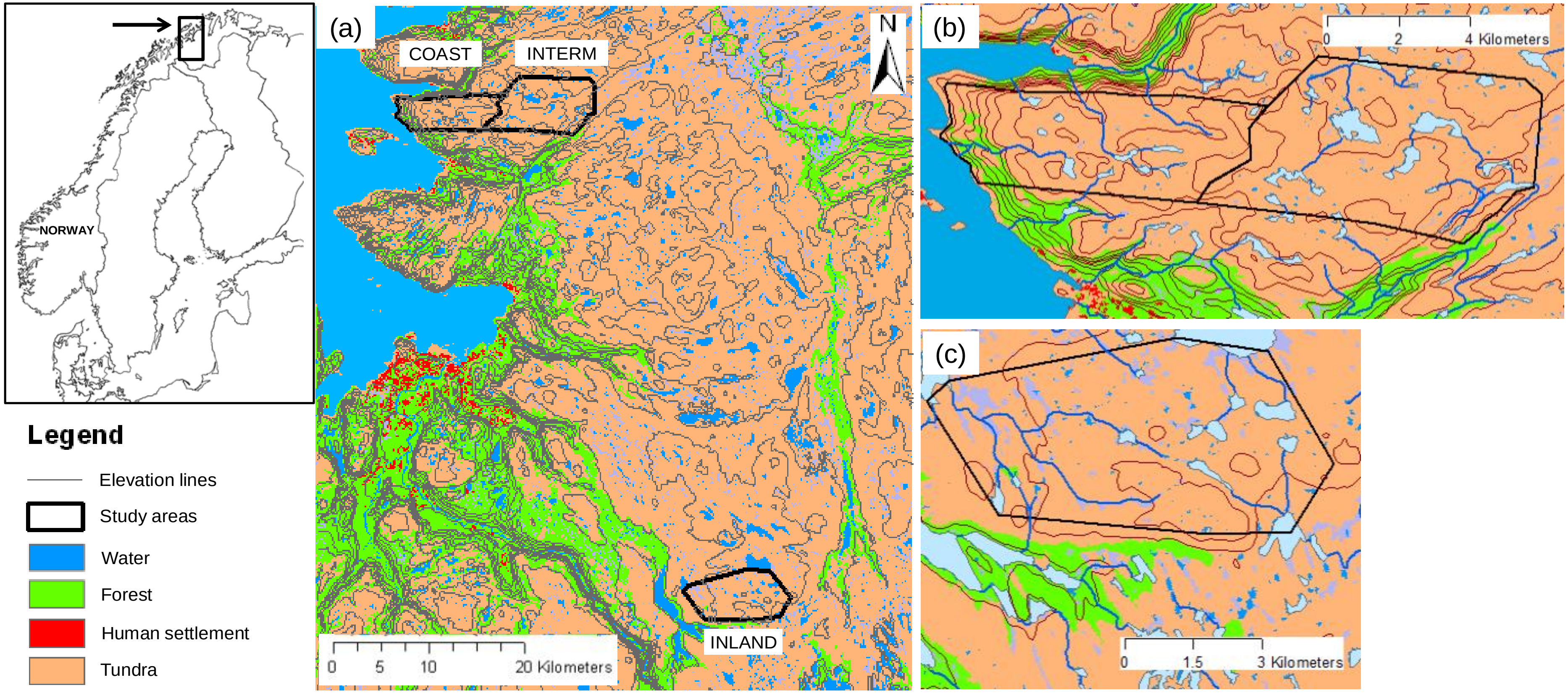

NORWAY
Legend
Elevation lines
Study areas
Water
Forest
Human settlement
Tundra
(a)
COAST
INTERM
INLAND
N
0 5 10 20 Kilometers
(b)
0 2 4 Kilometers
(c)
0 1.5 3 Kilometers

Figure 2

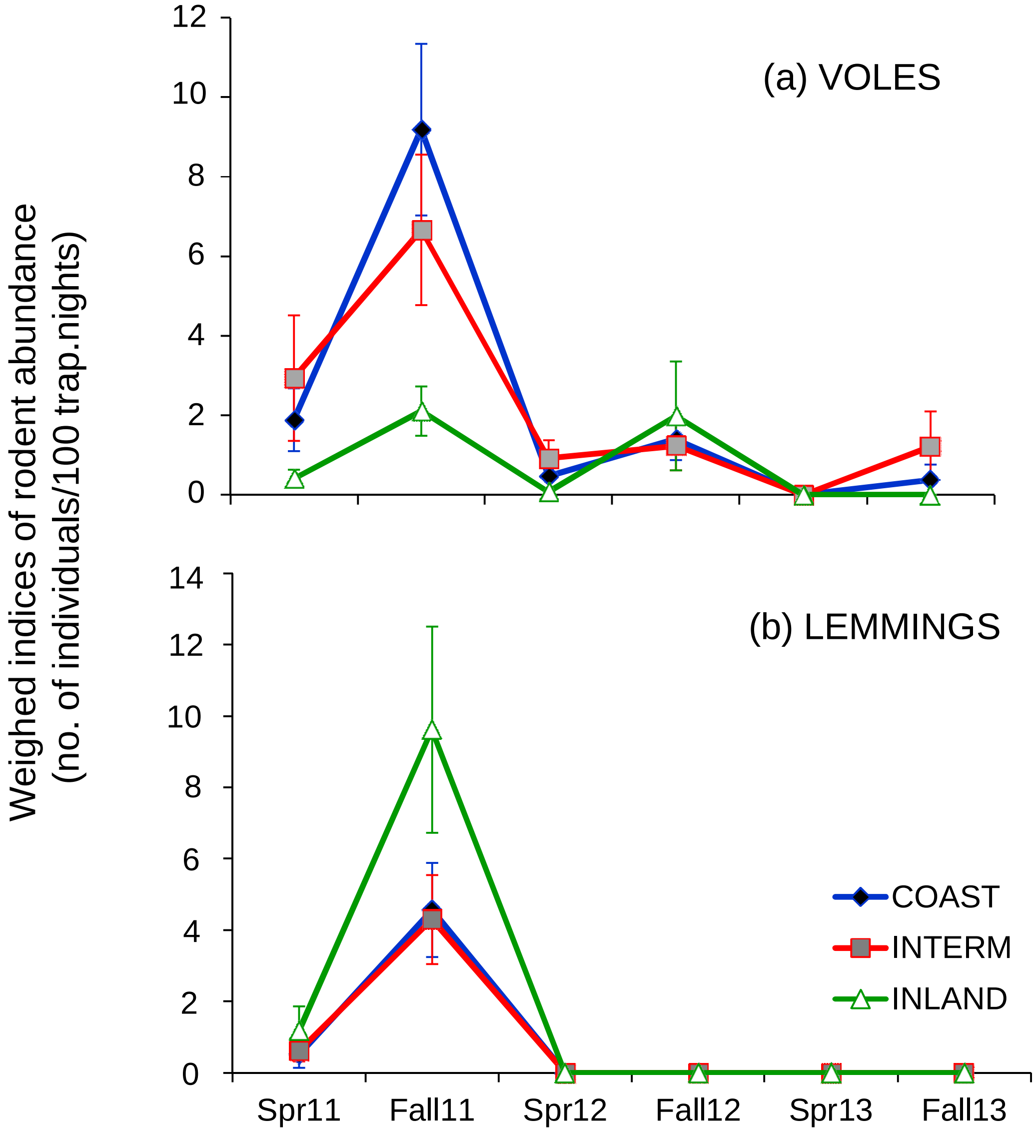
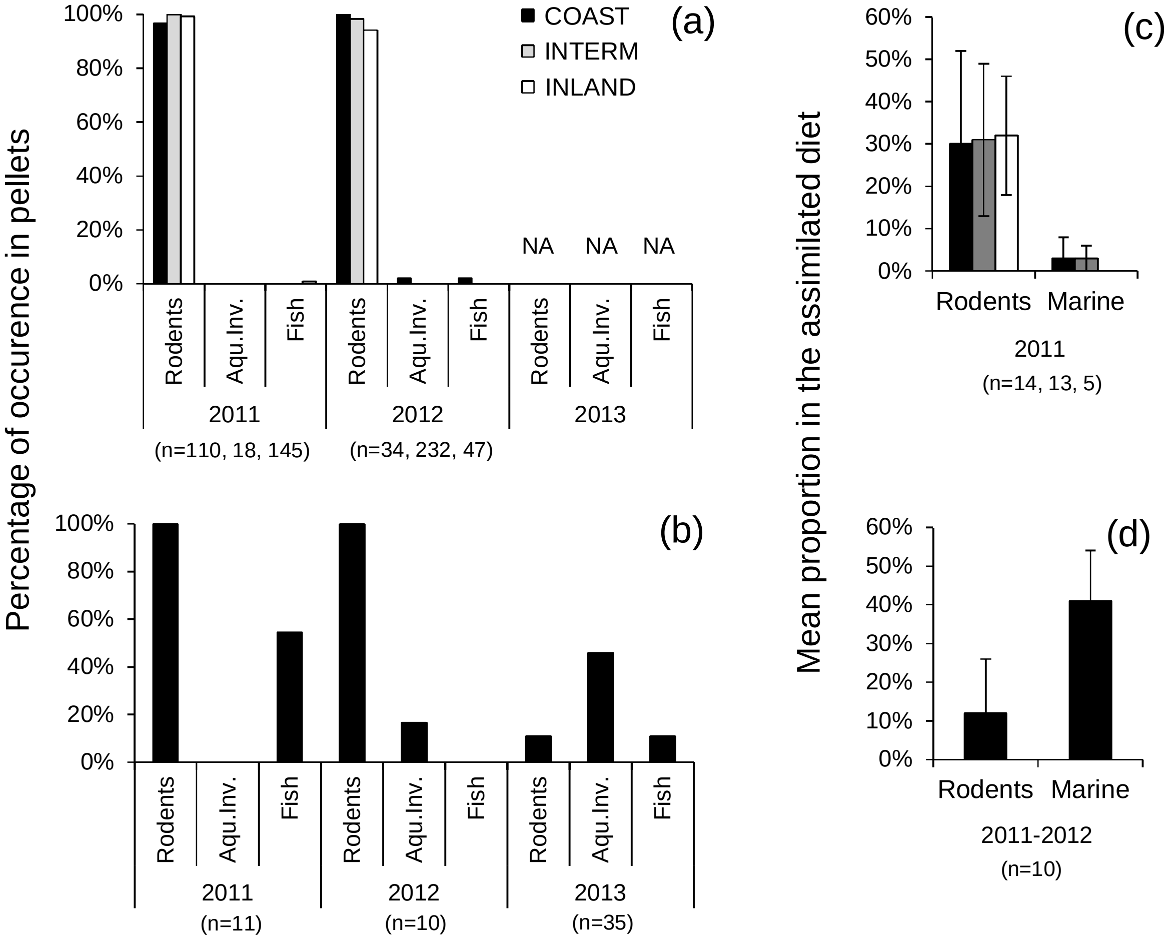

Weighed indices of rodent abundance
(no. of individuals/100 trap.nights)
(a) VOLES
12
10
8
6
4
2
0
(b) LEMMINGS
14
12
10
8
6
4
2
0
COAST
INTERM
INLAND
Spr11
Fall11
Spr12
Fall12
Spr13
Fall13

Figure 3



Percentage of occurence in pellets
100%
80%
60%
40%
20%
0%
■ COAST
▨ INTERM
☐ INLAND
(a)
NA
NA
NA
Rodents
Aqu.Inv.
Fish
Rodents
Aqu.Inv.
Fish
Rodents
Aqu.Inv.
Fish
2011
2012
2013
(n=110, 18, 145)
(n=34, 232, 47)
(b)
Rodents
Aqu.Inv.
Fish
Rodents
Aqu.Inv.
Fish
Rodents
Aqu.Inv.
Fish
2011
(n=11)
2012
(n=10)
2013
(n=35)
Mean proportion in the assimilated diet
(c)
60%
50%
40%
30%
20%
10%
0%
Rodents
Marine
2011
(n=14, 13, 5)
(d)
60%
50%
40%
30%
20%
10%
0%
Rodents
Marine
2011-2012
(n=10)

Figure 4

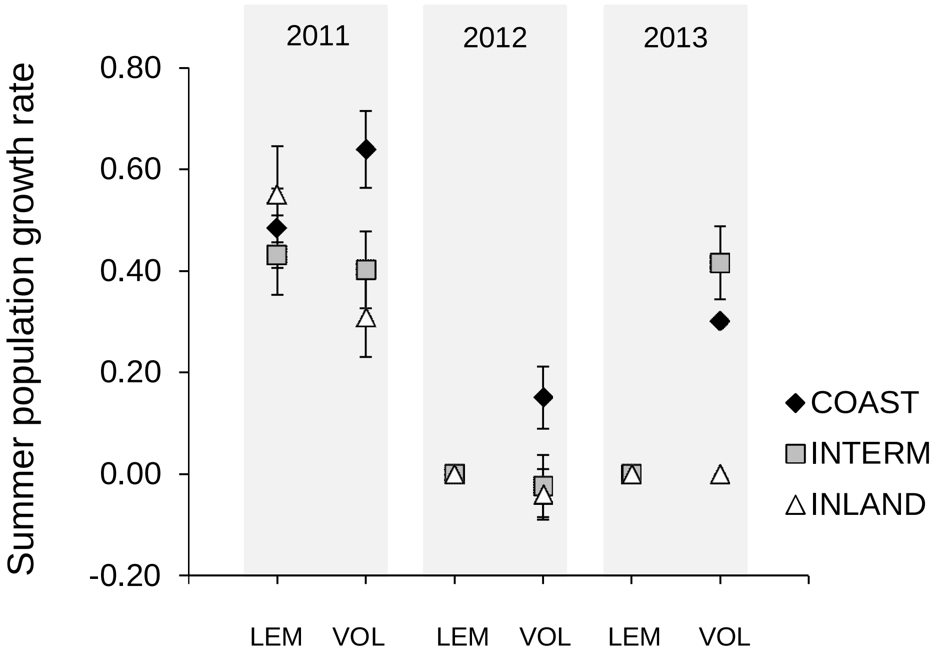

2011
2012
2013
Summer population growth rate
0.80
0.60
0.40
0.20
0.00
-0.20
LEM
VOL
LEM
VOL
LEM
VOL
◆ COAST
▨ INTERM
△ INLAND

Figure 5

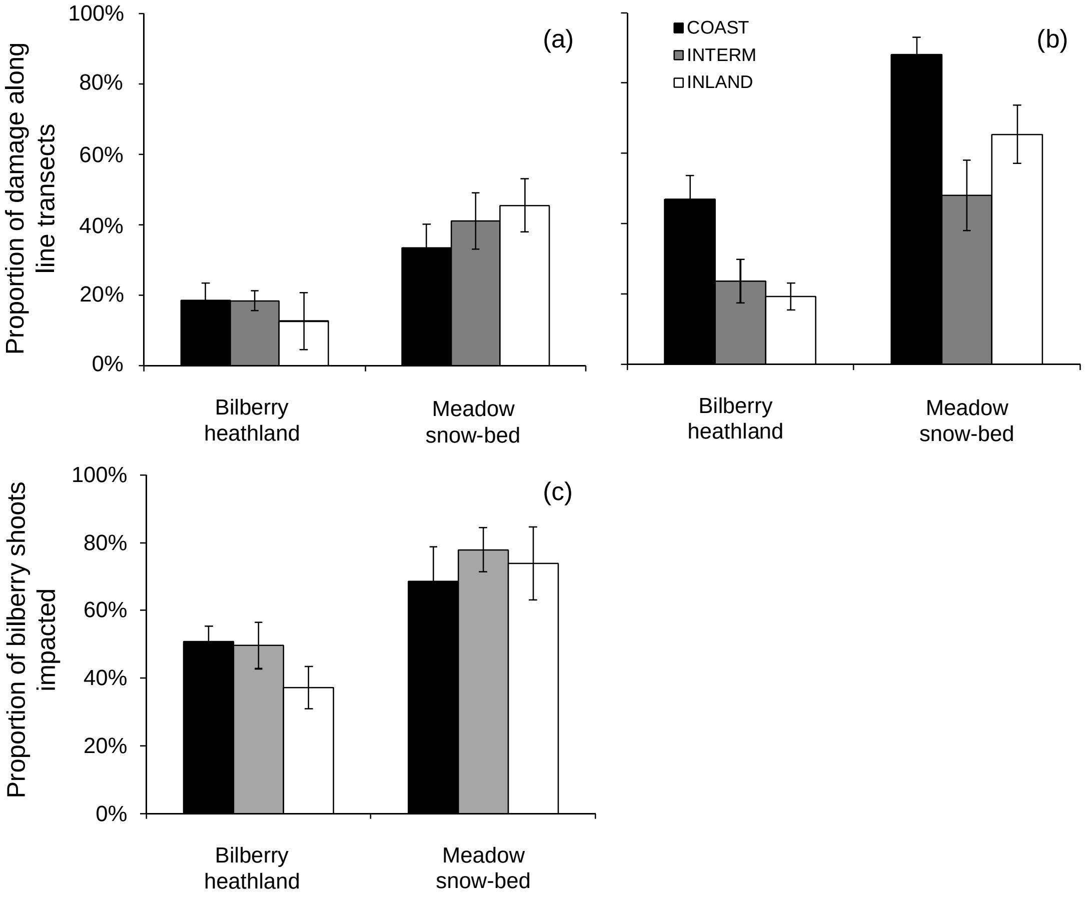
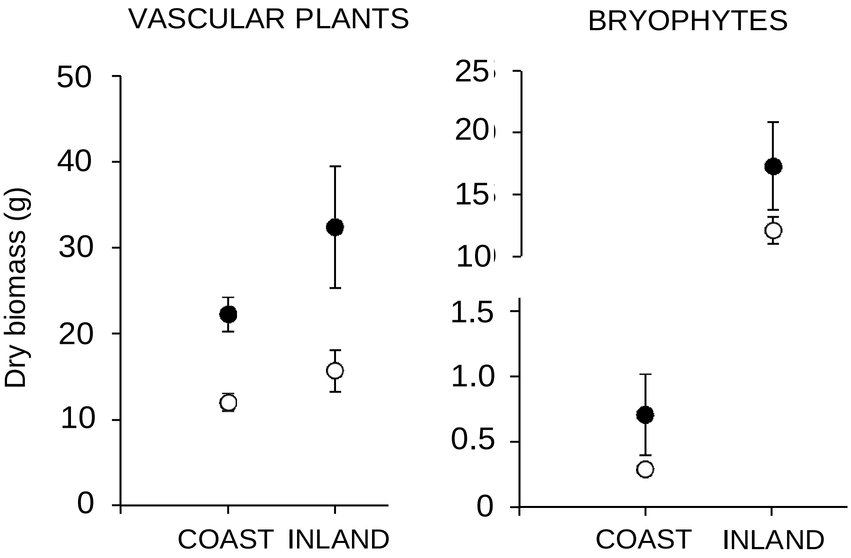

Proportion of damage along line transects
100%
80%
60%
40%
20%
0%
(a)
(b)
■ COAST
▨ INTERM
☐ INLAND
Bilberry heathland
Meadow snow-bed
Bilberry heathland
Meadow snow-bed
Proportion of bilberry shoots impacted
100%
80%
60%
40%
20%
0%
(c)
Bilberry heathland
Meadow snow-bed

Figure 6


VASCULAR PLANTS
BRYOPHYTES
Dry biomass (g)
50
40
30
20
10
0
COAST
INLAND
25
20
15
10
1.5
1.0
0.5
0
COAST
INLAND