Vole and lemming activity observed from space.

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Vole and lemming activity observed from space: vegetation cycles at a regional scale.

Predicting impacts of present global warming requires an understanding of the factors controlling plant biomass and production. The extent to which they are controlled by bottom-up drivers like climate, nutrient and water availability, and by top-down drivers like herbivory and diseases in terrestrial systems is still under debate[1]. By annually recording plant biomass and community composition in grazed control plots and in herbivore-free exclosures, at twelve sites in a subarctic ecosystem, we were able to show that the regular interannual density fluctuations of voles and lemmings drive synchronous interannual fluctuations in the biomass of field layer vegetation (Fig. 1). Plant biomass in the field layer was between 12 and 24% lower the year after a vole peak than the year before, and the combined vole and lemming peaks are visible as a reduced Normalized Difference Vegetation Index (NDVI) in satellite images over a 770 km^2 area in the following year, despite the wide range of abiotic, biotic and anthropogenic forces that influence the vegetation[2,3,4,5]. This strongly suggest that the cascading effect of rodents for the function and diversity of tundra plant communities needs to be included in our scenarios of how these ecosystems will respond to environmental changes.

It is well documented that the abundance of primary producers can be controlled by either abiotic factors like nutrients, water and temperature, or by biotic factors like herbivory and parasitism, but the relative importance of these two forces and how they vary between ecosystems and biomes are still under debate[1]. Recent climate changes put a new focus on these questions, since the projected responses of higher trophic levels have to be considered to accurately predict the abundance of primary producers in systems where biotic factors dominate[3,6].

In arctic ecosystems, where environmental conditions are harsh, abiotic factors like temperature, nutrient availability and soil disturbance limit the abundance of plant biomass[4,7]. However, herbivores also have strong effects on primary producer abundance in arctic ecosystems[6,8], and at the tree-line they can be more important than recent increases in temperature[9]. It is thus central to consider plant-herbivore interactions and thus the population dynamics of herbivores, in order to understand how arctic plant communities will respond to a climate change and also in interpreting recently observed changes[6,10].

Small rodents, especially voles and lemmings, are important herbivores in northern ecosystems[8,10,11,12,13,14,15,16,17]. In most boreal and arctic ecosystems, rodents normally experience regular interannual population density cycles of 3-5 years[13,18,19]. Recent studies suggest that a changing climate may lead to a disappearance of pronounced rodent cycles in the future[18,19], with severe negative consequences for predators and reduced consumer pressure for plants[6,18]. Since the densities of rodents fluctuate between years, so should their impact on the vegetation. The severe effect of small rodents on the vegetation in the winter after autumn peak densities is well documented[11,12, 14,15,16,17]. However, there are still many challenges remaining in order to understand how changing rodent cycles would influence arctic plant communities. One challenge is that the long-term effect of rodents depends both on the resistance and tolerance of the vegetation to herbivory, meaning that both plant vulnerability during peak densities and the ability of plants to re-grow between peaks matters[20]. However, the only time series with annual records of plant responses that are long enough to record the dynamic responses of plant communities to rodent cycles (8 years), lack matching data from exclosures[21,22] and thus the power to test whether plants or herbivores are driving these interactions. Another major challenge is that the effect of rodents is typically very heterogeneous at various spatial scales within and between habitats[8]. It has thus been difficult to estimate the effects of rodents at spatial scales relevant for regional or global predictions of ecosystem responses to environmental changes. Our study overcomes both these challenges by a) presenting a 14-year time series of plant abundance in grazed control plots and herbivore-free exclosures, which shows that rodents drive cycles in plant abundance, and that the amplitude of these cycles depends on plant traits, and b) combining the results with NDVI estimates from satellite images, which show that these cycles are important at a landscape scale.

The vole population fluctuated with a three year cycle throughout the study period (1998-2011), with pronounced peaks in 2001, 2004, 2007 and 2010 (Fig. 1a, Table 1).The fluctuations of lemmings were both larger in amplitude and less regular than the vole cycles. (Fig. 1b). Lemming peaks were recorded in 2001, 2007 and 2010, and were always synchronous with a vole peak. The lemming peak in 2001 was much smaller than the later peaks. There was also a vole and lemming peak in the region in 1997, the year before our trapping started (pers. obs.). The rodents reduce plant biomass in this ecosystem, since plant biomass increased substantially between 1998 and 2011 in plots where herbivores had been excluded, compared to grazed control plots (Fig 1c, Table 1).

Plant biomass in the grazed plots fluctuated synchronously with the rodent densities, with peaks in 2001, 2004, 2007 and 2010, and distinctive declines in the year after the peaks (Fig 1c). Ground truth measurements of NDVI in 2011 in the plots used for permanent vegetation recordings revealed a higher NDVI inside the exclosures than in the grazed controls and a positive linear relationship between plant biomass and NDVI (Supplementary Figure 2). It should thus be possible to detect the effects of rodents on the vegetation at larger spatial scales using satellite images. The distinct decline of plant biomass the year after a rodent peak could indeed be observed as a decline of regional NDVI estimated from satellite images, but only when there had been a combined vole and lemming peak (Fig.1a, Fig. 1b, Fig. 1d). NDVI estimated in a homogenous heathland area close to the oceanic location (Fig. 1d; Supplementary Figure 1) was reduced by the combined vole and lemming peaks of 2002, 2008 and 2011 by 8%, 25% and 31% respectively. When NDVI was estimated for the whole study region (770 km^2 including forest and mountains, Supplementary Figure 1), only the large lemming peaks (2007 and 2011) were clearly detectable (25%, 19% respectively). Spectral analyses showed that rodents, NDVI, and abundance of most species fluctuated with 3-year cycles, although the fluctuations were only significant for rodents, total plant biomass and *Vaccinium myrtillus* (Table 1). Moreover, pair-wise cross correlation analyses show that both plant biomass in grazed control plots and NDVI estimated from satellite images fluctuated in synchrony with the combined vole and lemming densities (Table 1). The 1 year lag phase between rodent density and plant biomass might be counter-intuitive, but is explained by the fact that the rodents have the strongest impact on their food plants during the winter[12,18,19] and plant biomass was recorded in the summer. The effect of rodents is thus recorded as a decrease in biomass the year after the peak. Plant biomass increased linearly in the herbivore-free exclosures, with pronounced dips in 2004 and 2008, potentially explained by an *E. autumnata* outbreak and an extreme winter event, respectively (Supplementary Table 1).

The pronounced effect of rodents on the vegetation is also demonstrated by the significant log linear relationships between plant biomass and the number of years since a vole peak (Fig. 2a, r^2=0.59, P=0.001). NDVI of the 20km^2 heathland area and the whole study region (770km^2) were also log linearly related to years since a combined vole and lemming peak (Fig. 2b;

r^2=0.60, P=0.003; r^2=0.45, P=0.017). Log-linear relationships were stronger than linear ones indicating that the rate of recovery decreased over time.

Rodents influenced the abundance of all dominant field layer plants. Four out of six dominant plant species increased significantly in plots where herbivores were excluded (Fig 3a-d, Table 1). Both highly preferred forage species like the deciduous shrubs *Betula nana* and *Vaccinium myrtillus*[12] and low quality forage species like the evergreen shrubs *Empetrum hermaphroditum* and *Vaccinium vitis-idaea*[12] increased in exclosures. Spectral analyses indicated that all dominant species, except *B. nana* and *D. flexuosa*, fluctuated with a three year cycle. Cross-correlation analyses indicate that all these four shrub species fluctuated in synchrony with the rodent population. *V. myrtillus* and *V. uliginosum* decreased the year after a rodent peak as indicated by the negative correlation with a one year lag phase. *Empetrum hermaphroditum* and *Vaccinium vitis-idaea* were instead positively correlated with rodent densities without a lag phase (Fig. 3c,e-f; Table 1).

Our data show for the first time that vole and lemming cycles cause cascading cycles of plant biomass in tundra ecosystems, and that these cycles are strong enough to be detectable from moderate resolution satellite imagery like Terra/Aqua MODIS at landscape scales. Strong effects of voles and lemmings are not a new finding since consumption of 20%-100% of the aboveground biomass is frequently reported from various places in the circumpolar tundra [10,11, 12,14, 16, 17]. However, our novel finding is that voles and lemmings can have strong effects on the plant biomass even at a landscape scale and that they drive interannual cycles in plant biomass and species composition. Furthermore, our results show that although palatable species fluctuated more than unpalatable species, the unpalatable *E. hermaphroditum* increased the most in the exclosures, thereby high-lighting the importance of rodents in determining plant community composition during climate warming.

Although the notion of rodent-driven fluctuations of NDVI is completely novel, it is well known that anthropogenic and biotic interactions may cause changes in NDVI that obscure the expected climate-NDVI relationships[2]. For example, NDVI and plant biomass in the region were severely reduced by an autumnal moth outbreak in 2004[5,23] (Supplementary Table 1). This, together with the lower amplitude of the rodent peak in 2004 (Fig. 1a), can explain why NDVI declined less than after the other peaks. On the other hand, in 2008, the NDVI declined more than expected based on rodent densities alone (Fig. 1c, Fig. 2b). The NDVI was probably reduced both by the rodent peak and by an extreme winter-climate event that caused massive mortality of dwarf-shrub vegetation in 2008[2,24].

Although there are numerous abiotic, biotic and anthropogenic factors operating simultaneously to control plant biomass[25] and NDVI[26], the effects of rodent cycles *per se* are strong enough to create predictable cycles in plant abundance, recorded both as plant biomass in small permanent plots, and as NDVI estimated from satellite images. These results are important for predicting the effects of climate change on northern ecosystems, since disappearing vole and lemming cycles have been linked to climate change[18,19], and the cascading effects of disappearing cycles for diminishing predator populations have been frequently discussed[6,18]. Our results reinforce the importance of rodents by showing that they create vegetation cycles and plant community changes as well. Although the importance of these cycles for biodiversity and ecosystem functioning of the tundra remain to be investigated, it is clear that the cascading effect of rodents for the function and diversity of tundra plant communities needs to be included in our scenarios of how these ecosystems will respond to environmental changes, and interpreting causes of recently observed vegetation changes.

Furthermore, our evidence that the relationship between NDVI values and biomass is affected by changes in plant community composition highlights that caution should be used in assuming biomass changes from satellite-derived NDVI values alone. Although plant biomass and NDVI were positively related in plots recorded in this heathland in 2011, the trend over time is different. While plant biomass has a slight positive trend, NDVI decreases. The species-specific shifts in vegetation over time presented in Fig. 3a-f might be the main reason for the slight reduction of regional NDVI (Fig. 1d) over the same period. The spectral reflectance of the main species that increased in biomass (*B. nana)* is low compared with the species that decreased most (*V. myrtillus*). Therefore, NDVI differences integrate changes in overall biomass and species-specific changes in biomass[23,27]. Hence, caution should be used in assuming large scale changes in biomass without prior knowledge about the changes in the in situ species composition.

METHODS

We studied the effect of rodent cycles on subarctic vegetation in the Abisko region, in northernmost Sweden by combining 1. yearly vegetation recordings inside and outside replicated rodent exclosures (1998-2011) during a period of accelerating climate warming, 2. data from monitoring vole populations (1998-2011) and 3. NDVI estimates from satellite imagery (Modis) of the study sites, a 20 km^2 area dominated by tundra heathlands and from the whole study region (770km^2). NDVI (Normalized difference vegetation index) is a method to measure the amount of photosynthesizing vegetation by studying the spectral reflection of red and near infrared radiation[2]. NDVI estimated from satellite images has frequently been used to study large scale vegetation changes in the Arctic from regional[28] to circum-polar scales[28]. Twelve, 8m×8m vole exclosures and 12 control plots, situated in two different locations, Vassijaure (68°26′26″N, 18°16′29″E) and Paddus (68°19′23″N, 18°51′57″E), and two different habitats (tundra/forest) were used to quantify interannual variations and possible trends in impacts of rodents on biomass. The vegetation was recorded annually in three 0.5m×0.5m permanent subplots inside each experimental plot using the point-quadrate technique and transformed into plant biomass using transfer functions. See Supplementary Information|Methods section for further details.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature

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Author Contribution J.O. has managed the long-term herbivore exclosure experiment and performed plant measurements in the field. H.T. performed the image processing and the NDVI estimations from satellite images. J.O. performed the statistical analyses and wrote the manuscript, to which all authors contributed with discussions and text.

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Figure legends

Figure 1. Microtine rodent densities, plant biomass in grazed control plots and NDVI estimated from satellite images fluctuated with 3 year cycles in the Abisko Region in northern Sweden between 1998 and 2011. a, The vole catch rates (number caught per 100 trap nights; green, spring; red, fall). b, The lemming catch rates (number caught per 100 trap nights; green, spring; red, fall). c. The plant biomass (g/m^2) in grazed control plots (red, triangles) and herbivore-free exclosures (blue, dots). The small dots represent ±1SE d, circles represent NDVI of a 20km^2 area dominated by open heathland habitats in the same region where rodents were trapped and rodent exclosures were established. Triangles represent the NDVI of the 770 km^2 study area.

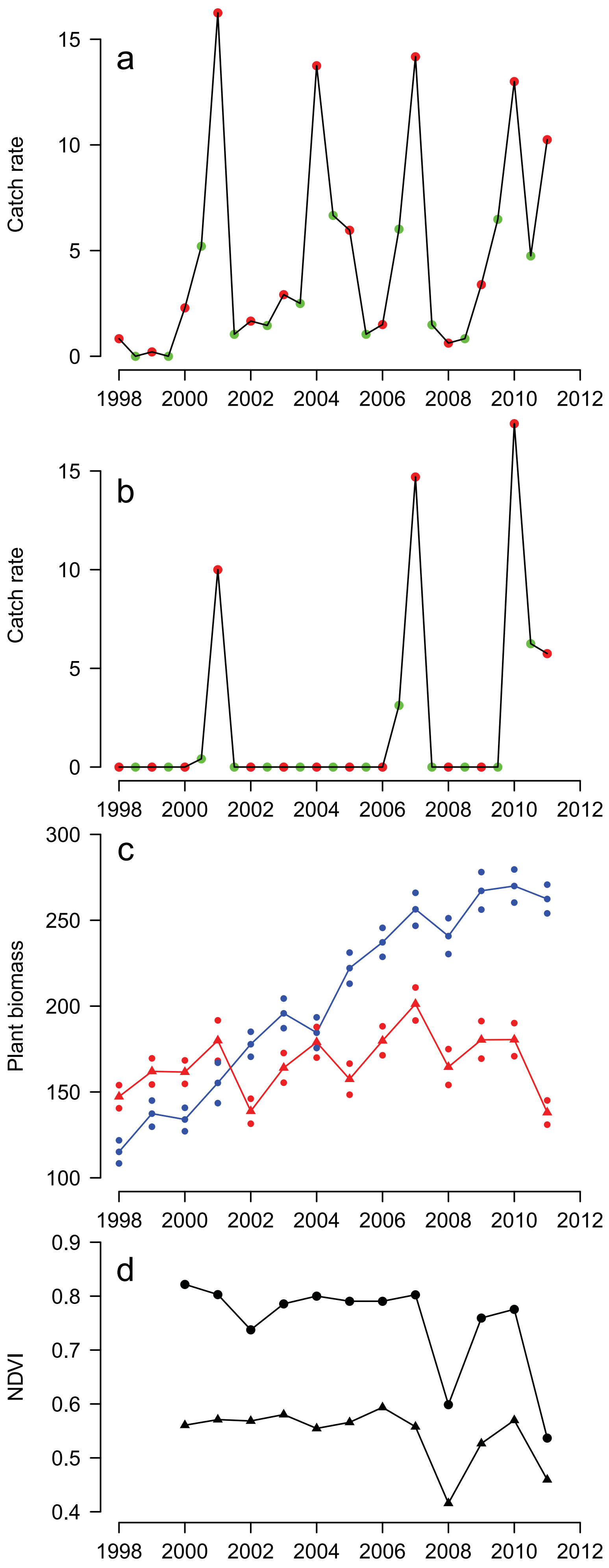
Figure 2. The rodent cycles drive cycles in plant biomass and NDVI a, Plant biomass (g/m^2) in grazed control plots was significantly related to number of years since a vole peak. b, NDVI estimated from satellite images was significantly related to the number of years since a combined vole and lemming peak. Circles represent NDVI of a 20km^2 area dominated by open heathland and triangles represent the NDVI of the 770 km^2 study area. Log-linear relationships had a better fit to the data than linear relationships in all three cases, indicating that the recovery rate of plant biomass and NDVI decreased over time.

Figure 3. Plant biomass of the dominant plant species in grazed control plots (red, triangles) and herbivore-free exclosures (blue, dots) between 1998 and 2011. a. *Betula nana*, b. *Deschampsia flexuosa*, c. *Empetrum nigrum*, d. *Vaccinium myrtillus*, e. *Vaccinium uliginosum*, f. *Vaccinium vitis-idaea*. The small dots represent ±1SE

Table 1 Results from statistical analysis.

	Year×Treatment		*Spectral*	*Cross-correlation*	
Species	$F_{1,268}$	P	*density*	Lag	r
Rodents			**3**		
NDVI heath			3	1	**-0.81**
NDVI			3	1	**-0.68**
Plant Biomass	**114**	**>0.001**	**3**	1	**-0.66**
Betula nana	**2.7**	**0.002**			
Deschampsia flexuosa	1.1	0.794			
Empetrum hermaphroditum	**2.7**	**>0.001**	3	0	**0.54**
Vaccinium myrtillus	**5.5**	**>0.001**	**3**	1	**-0.63**
Vaccinium uliginosum	0.4	0.134	3	1	**-0.65**
Vaccinium vitis-idaea	**2.5**	**>0.001**	3	0	**0.54**

The effect of excluding herbivores on the dominant plant species were significant (bold font) for total biomass and most taxa (Year×Treatment). Rodents, NDVI estimates and most plant species had a spectral density of 3 years, but the effects were only significant for total rodent density, total plant biomass and *Vaccinium myrtillus*. Cross-correlation analyses reveal that NDVI and most plant species had a positive relationship to rodent densities without any lag phase, or a negative relationship with one year lag phase.


a
Catch rate
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b
Catch rate
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2000
2002
2004
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2010
2012
c
Plant biomass
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150
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2006
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d
NDVI
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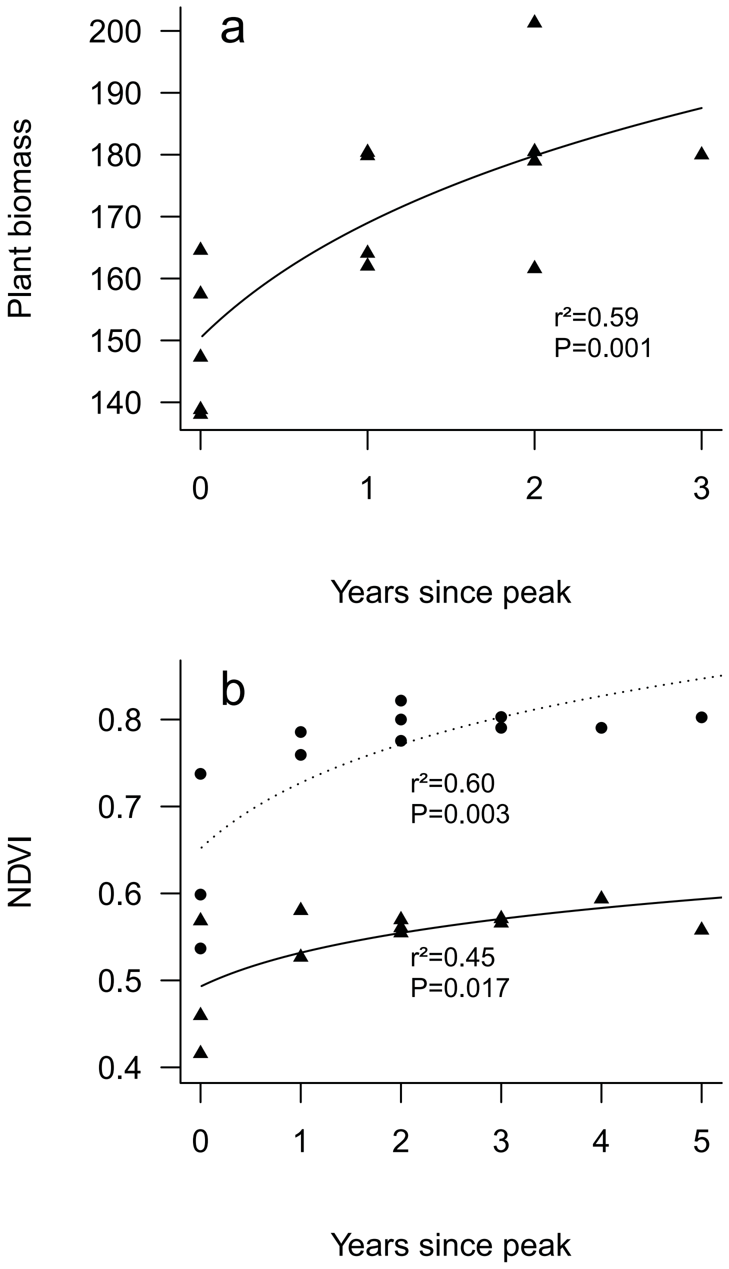
a
Plant biomass
200
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180
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160
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r²=0.59
P=0.001
Years since peak
b
NDVI
0.8
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0.5
0.4
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3
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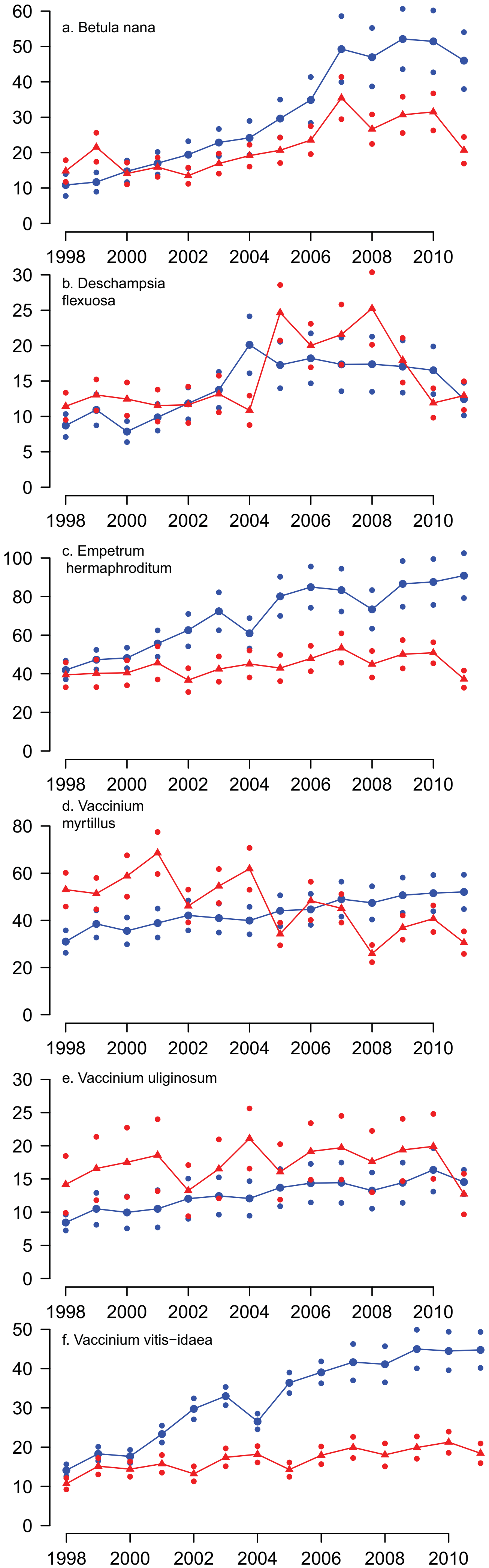
5
r²=0.60
P=0.003
r²=0.45
P=0.017
Years since peak


a. Betula nana
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b. Deschampsia flexuosa
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c. Empetrum hermaphroditum
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d. Vaccinium myrtillus
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e. Vaccinium uliginosum
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f. Vaccinium vitis−idaea
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2002
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Supplementary Information: **Vole and lemming activity observed from space: Vegetation cycles at a regional scale.**

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Supplementary Methods

Study area

The study was carried out in the Torneträsk region, between Abisko and the Norwegian border. The experimental part of the study was carried out in two locations along a continental–oceanic climatic gradient within the forest–tundra ecotone (Supplementary Fig. 1). Both study locations are situated on nutrient-poor bedrock and the forest is dominated by mountain birch (*Betula pubescens* ssp. *czerepanovii*), which is typical for Fennoscandian tree lines. The continental location is situated in the proximity of the Paddus cliff about 4 km southwest of the Abisko Scientific Research Station, Sweden at 68°19′23″N, 18°51′57″E. The mean annual air temperature (1960-1990) at the Abisko Scientific Research Station is -0.8°C and mean annual precipitation for the same period is 304 mm. The study location consists of a mixture of forest and tundra patches. The birch density in the forest patches was 747 ± 68 trees ha^{-1}. Reindeer graze in the area mainly in spring and autumn, but solitary reindeer can be found throughout the summer. The oceanic location is situated east of the lake Vassijaure, Sweden, at 68°26′26″N, 18°16′29″E. The mean annual temperature at the nearest climate station, Katterjokk, is -1.7°C and the mean annual precipitation is 848 mm (1960–1990). The vegetation consists of a mixture of forest patches, open heathlands and mires. The average birch density is 1997 ± 340 trees ha^{-1}. See[1,2] for a more detailed description of the study sites. Climate warming in this region since 2000 has reached a level where current warming exceeds earlier warm periods and has crossed the 0°C mean annual temperature threshold[3]. Since the 1980's, the previous century-long trend of increase in snow thickness has been replaced by an accelerating decrease[3,4].

Experimental design

We chose six study sites within each study location, three in the birch forest and three in the tundra. The field-layer vegetation consists of dwarf shrub heath in all sites, but grasses and herbs were more common in the forests. We established 8 m × 8 m experimental plots in each forest and tundra site (24 in total) and randomly assigned these plots for one of the following treatments; controls where all herbivores have access to the vegetation and small mesh size exclosures that exclude all mammalian herbivores. The small mesh size exclosures were constructed from galvanized net with a mesh size of 1.2 cm × 1.2 cm (height 1 m) dug down into the mineral soil (10–30 cm). As voles and lemmings were the most important small vertebrate herbivores in this region[1], we will refer to them as 'rodent exclosures'. Two rodent exclosures were destroyed by frost heaving in the oceanic location and all data presented in this paper are thus based on four of the rodent exclosures from this location. The original experiment also includes large mesh size exclosures that exclude only reindeer and two more study locations in Northernmost Norway[1,2]. No data from these two locations or for the large mesh size exclosures are included in the present paper. It is unlikely that the fences significantly affected snow depth.

Vegetation recording

We recorded the plant community composition in three permanent subplots in each exclosure and control plot and we estimated plant biomass non-destructively with a modified point intercept method[5]. We carried out the measurements annually from 1998 to 2010, in late July–early August, using a transparent plexi-glass table, 0.5 m × 0.5 m, with 100 randomly distributed 4 mm holes. We lowered a pin of the same diameter through each hole, and recorded the number of contacts the pin made for each vascular plant species in the vegetation beneath it. To convert the point intercept data to biomass for the permanent vegetation plots, 20 additional representative plots were selected in the summer 2011, recorded by the point intercept method and harvested at the peak of the growing season (early august). The plant biomass was sorted into functional groups, and dried to constant weight (48 hours at 60°C) before being weighed.

NDVI Estimates

NDVI (Normalized difference vegetation index) is a method to measure the amount of photosynthesizing vegetation by studying the spectral reflection of red and near infrared radiation. NDVI estimated from satellite images has frequently been used to study large scale vegetation changes in the Arctic[6,7,8,9,10,11]. We extracted NDVI-values a) from the sites Vassijaure (0.64km^2)

and Paddus (0.43km^2), b) from a 20km^2 area situated between 68°30′15″N, 18°19′47″E in NWest to 68°28′ N, 18°23′25″E in SEast, and c) the whole study area between 68°31′30″N, 18°11′15″E in NWest to 68°18′ N, 18°51′51″E in SEast including a more complex set of habitats (Supplementary Fig. 1). The 20km^2 area for the NDVI analyses was chosen to be large, continuous, dominated by tundra heathland with only scattered fragments of forest, and close to the sites where the rodent densities were monitored and the exclosure study was carried out. NDVI data covering periods of 16 days (centred on mid-July) were obtained from the MODerate-resolution Imaging Spectroradiometer (MODIS) sensors on NASA's Terra satellites (the MOD3A1 and MOD13Q1 products[33]. Since satellite data with medium to high spatial resolution (SPOT, IRS-P6 and Landsat TM/ETM+) do not exist for the peak summer season annually due to extensive cloud cover, the 16-day NDVI data product was found to be the most optimal in this part of the world [35]. We checked past July NDVI values for the study area for all years that data from MODIS sensors are available (2000-2011). NDVI measurements made by SPOT-5, Landsat-5 TM, Landsat-7 ETM+ and IRSPS6 LISS-3 in July 2007 and 2008, respectively, were consistent with the MODIS-based measurements supporting the validity of the latter. For example Landsat 7 ETM+ showed a significant reduction of NDVI for the alpine heathland including our site in Vassijaure from 0.39 +/-0.14 in July 2007 to 0.05 +/- 0.16 in July 2008 and back to 0.43 +/-0.10 in July 2009. The same area for Vassijaure based on MODIS was 0.70 +/-0.01 in 2007, 0.54 +/-0.03 in 2008 and 0.65 +/-0.03, respectively[6,12]. To verify that NDVI reflects plant biomass in our study system (plot scale)[12], NDVI was measured in our 0.25m^2 plots for permanent vegetation recording using a NDVI Digital Camera 12 MP DSLR and Win CAM Regular software (Regent Instruments Inc, Quebec, Canada).

Herbivore densities

We monitored spring and fall densities of rodents, with the small quadrat method[34,35], with replicated quadrats of 15 m × 15 m, each with 12 snap traps set for a period of 48 h and checked twice. We started the trapping using 10 small quadrats in 1998 in both locations (five in forests and five in tundra). We thoroughly surveyed the research sites in June 1998, before the exclosures were built. Tracks, droppings, damaged plants and bodies of dead voles and lemmings were found. All these signs indicated that there was a rodent peak in the autumn of 1997. More than 80 % of all caught individuals of voles were *Myodes rufucanus.* In addition, Norwegian lemming, *Lemmus lemmus*, were abundant during peak years. A few individuals of *Myodes rutilus* and *Microtus agrestis* were also caught. This species composition is typical for dry heathlands in the Fennoscandina forest-tundra ecotone. There were severe outbreaks of the autumnal moth, *Epirrita autumnata*, in Abisko in 2004[7,8]. However, although large parts of the surroundings were totally defoliated, including most of the field layer, none of our study sites in the upper part of the forest–tundra ecotone were severely affected. Our study sites were all situated in areas classified as moderately defoliated or not defoliated, according to estimates from remote sensing[7,8] and tree ring studies[7].

Statistical analyses

The effects of excluding herbivores on plant biomass were tested with repeated measure ANOVAs. We examined the cyclic behavior of rodent and plant populations by spectral analysis. Since the time series are fairly short, populations were classified as cyclic if there was a peak in the spectral density between 2 and 5 years and as non-cyclic, if there was no peak in that interval. The synchrony between plant and rodent cycles was examined using cross-correlation analysis. The relationship between years since a vole peak and NDVI and plant biomass, respectively, were tested using linear regressions. Both linear and loglinear models were used and the model with the highest r^2 was selected. We also tested if including a range of climatic variables (mean summer temperature, degree days above 0ºC or +5 ºC or total summer precipitation) would improve the fit of these models. The fits of these models were compared using the Akaike Information Criterion. All statistical tests were performed within the statistical environment R[38].

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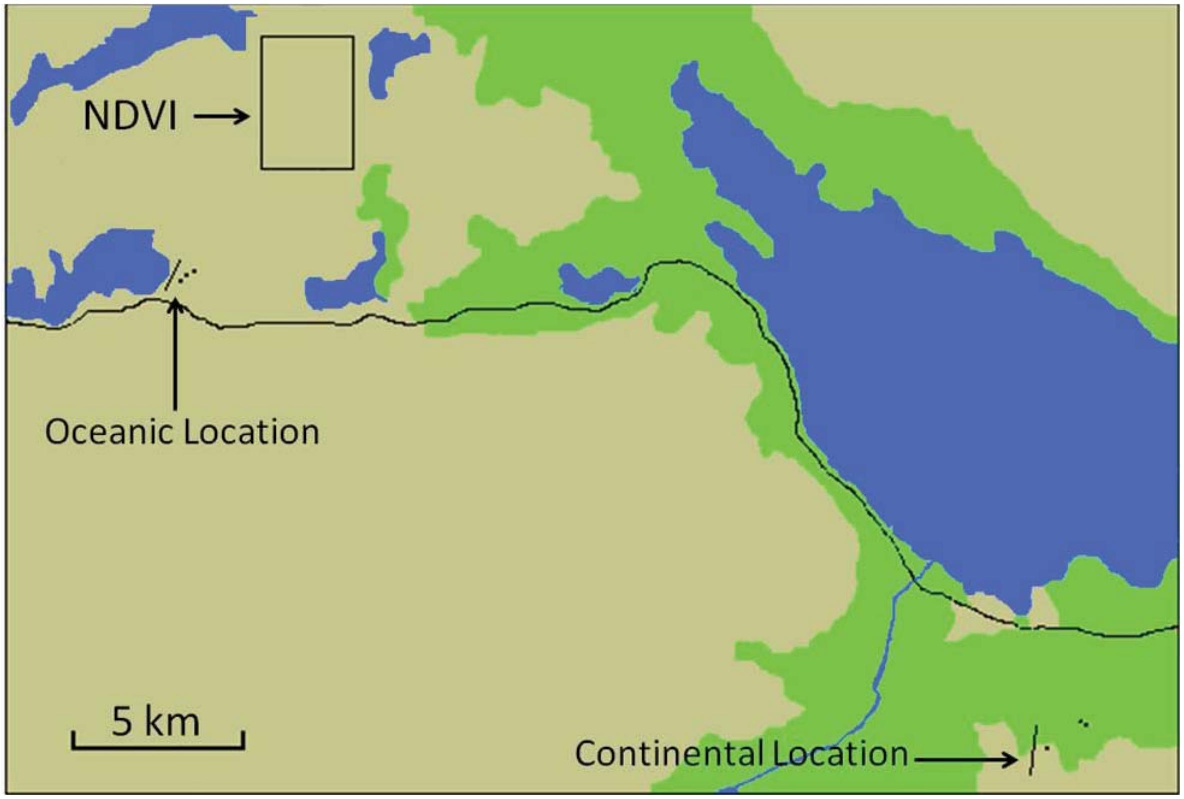
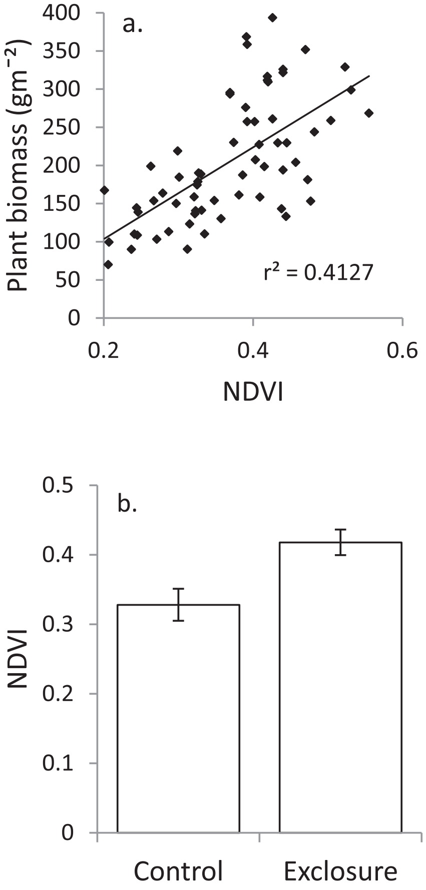
SUPPLEMENTARY INFORMATION

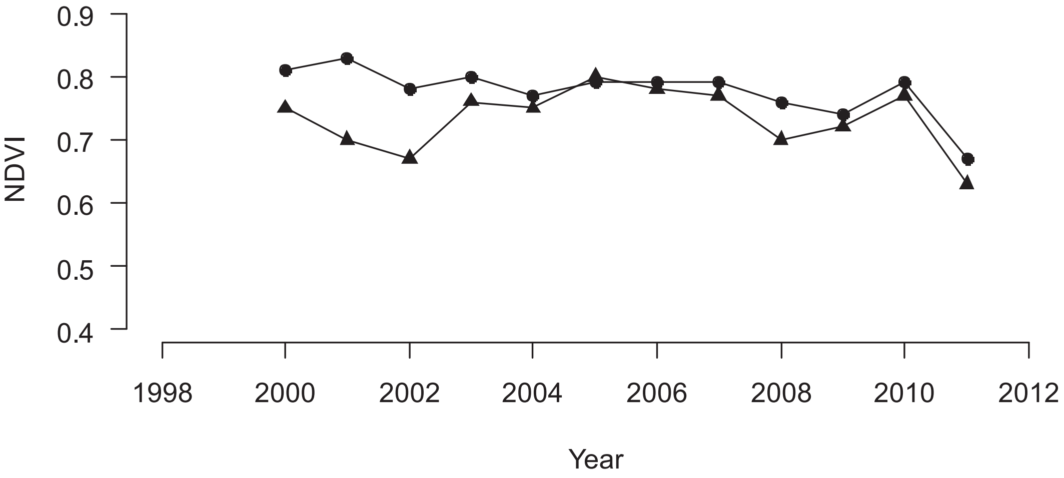
Supplementary Figure 1| Map of the study region. The large rectangle denotes the area selected from satellite images for NDVI estimates. The location of the rodent trapping transects (line) and the exclosures (dots) are also depicted in each of the two study sites.



Supplementary Figure 2| NDVI and plant biomass. a. The relationship between plant biomass and NDVI in the 0.25 m^2 subplots used for permanent vegetation recordings in 2011. b. the differences in NDVI between exclosures and control plots in the 0.25 m^2 subplots used for permanent vegetation recordings in 2011.



Supplementary Figure 3| NDVI estimated for the sites where the exclosures are situated ($0.21m^2$). Circles represent NDVI of a $0.42km^2$ area in which the exclosures in the continental location is situated. Triangles represent NDVI of a $0.63km^2$ area in which the exclosures in the oceanic location is situated.



Supplementary Table 1| Different factors that reduce plant biomass in this tundra ecosystem.

Year	98	99	00	01	02	03	04	05	06	07	08	09	10	11
Rodents					35			33			10			20
Reindeer	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Invertebrates	<2	<2	<2	<2	<2	<2	13	<2	<2	<2	<2	<2	<2	<2
Climatic events											10			

Estimated effects of different factors that reduce plant biomass in the investigated vegetation, presented as % reduction. The effect of rodents during peak years is calculated as the difference between the change in open plots and herbivore-free exclosures. The effects of reindeer are based on data from previously published studies from the same exclosures[2]. The effects of two important events, the large *Epirrita autumnata* outbreak in 2004 and the winter warming event in 2008[6] were calculated as the reduction of biomass in the herbivore free exclosures. Estimates of invertebrate herbivores during non-peak years are based on[13].