Climatic and biotic extreme events moderate long-term responses of above- and belowground sub-Arctic heathland communities to climate change

Running head: Interacting drivers of Arctic communities

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**Abstract**

Climate change impacts are not uniform across the Arctic region because interacting factors cause large variations in local ecosystem change. Extreme climatic events and population cycles of herbivores occur simultaneously against a background of gradual climate warming trends and can redirect ecosystem change along routes that are difficult to predict. Here, we present the results from sub-Arctic heath vegetation and its belowground micro-arthropod community in response to the two main drivers of vegetation damage in this region: extreme winter warming events and subsequent outbreaks of the defoliating autumnal moth caterpillar (*Epirrita autumnata*).

Evergreen dwarf shrub biomass decreased (30%) following extreme winter warming events and again by moth caterpillar grazing. Deciduous shrubs that were previously exposed to an extreme winter warming event were not affected by the moth caterpillar grazing while those that were not exposed to warming events (control plots) showed reduced (23%) biomass from grazing. Cryptogam cover increased irrespective of grazing or winter warming events. Micro-arthropods declined (46%) following winter warming but did not respond to changes in plant community. Extreme winter warming and caterpillar grazing suppressed the CO₂ fluxes of the ecosystem.

Evergreen dwarf shrubs are disadvantaged in a future sub-Arctic with more stochastic climatic and biotic events. Given that summer warming may further benefit deciduous over evergreen shrubs, event and trend climate change may both act against evergreen shrubs and the ecosystem functions they provide. This is of particular concern given that Arctic heath vegetation is typically dominated by evergreen shrubs. Other components of the vegetation showed variable responses to abiotic and biotic events, and their interaction indicates that sub-
Arctic vegetation response to multiple pressures is not easy to predict from single factor responses. Therefore, while biotic and climatic events may have clear impacts, more work is needed to understand their net effect on Arctic ecosystems.

Introduction

The Arctic regions are undergoing particularly rapid climate change compared to the rest of the world, but predicting the impacts of climate change on Arctic ecosystems is challenging. These challenges arise (in part) because (i) changes in the gradual climate are not uniform across the Arctic (AMAP 2011), and (ii) at local scales, ecosystem responses to warming are not necessarily the same due to variation driven by other biotic and climatic factors (Post et al. 2009; Callaghan et al. 2013). For example, the northward expansion of shrubs resulting in Arctic ‘greening’ that has arisen from gradual warming over the last decade has been observed in many locations but has not been uniform at local scales (Tape et al. 2006; Myers-Smith et al. 2011). This site specificity in plant community responses to climate warming is confirmed by a number of observations in northern Scandinavia (Hedenås et al. 2012; Callaghan et al. 2013). Warming of the Arctic is also expected to result in an increasing frequency of stochastic climatic events (Saha et al. 2006), such as extreme winter warming events. Such extreme events severely damage Arctic and sub-Arctic vegetation and can therefore, halt or reverse these ‘greening’ trends (Bokhorst et al. 2009; 2011; Callaghan et al. 2013; Bjerke et al. 2014). In addition, unpredictable population cycles of herbivores and fungal pests can severely affect the competitive interactions between plant species and readily change vegetation composition (Lehtonen and Heikkinen 1995; Malmström and Raffa 2000; van der Wal 2006; Jepsen et al. 2008; Van Bogaert et al. 2009; Olofsson et al. 2012; Jepsen et al. 2013; Karlsen et al. 2013). Plant community changes may affect belowground communities such as micro-arthropods that
in turn affect ecosystem processes. All these changes in community composition can alter feedbacks to the global carbon cycle (Cornwell et al. 2008; De Deyn et al. 2008). Predicting ecosystem change over northern lands is therefore particularly challenging given that these stochastic climatic events and herbivore outbreaks occur against a background of gradual warming trends.

To address the complexity of different drivers for communities and ecosystem processes in the Arctic we need to adapt our research to incorporate stochastic extreme events, as has been called for more generally in climate change research (Jentsch et al. 2007; Smith 2011) and in long-term monitoring programmes. Here we present the results from a sub-Arctic ecosystem that - following simulated extreme winter warming events in 2007, 2008 and 2009 (Bokhorst et al. 2011; 2012c)- was then subject to natural regional outbreaks of the defoliating autumnal moth (*Epirrita autumnata*) in 2012 and 2013. The extreme winter warming events were simulations of abrupt warm spells during winter, which are becoming more frequent in northern Scandinavia (Phoenix and Lee 2004; Johansson et al. 2011; Bjerke et al. 2014). These events can raise the mid-winter temperature to 10 °C and lead to snow melt across large (>1000 km²) areas (Bokhorst et al. 2009). Due to the loss of snow cover the vegetation and soil are exposed to colder freezing temperatures on the return of winter temperatures. This freezing leads to severe damage to the dominant dwarf shrubs *Empetrum nigrum*, *Vaccinium myrtillus*, and *V. vitis-idaea*, while other plant species such as the dwarf shrub *V. uliginosum*, and the grass *Deschampsia (Avenella) flexuosa* are much more tolerant (Bokhorst et al. 2011).

Aboveground, winter warming events may interact with outbreaks of the autumnal moth. This herbivore, in caterpillar form, typically feeds on leaves of birch (especially the widespread trees *Betula pubescens*), but once these have been consumed, dwarf shrubs are targeted (Jepsen et al. 2008) indicating that the shrub species are dually susceptible to climatic extreme events and herbivore outbreaks. Mosses – often a major component of high latitude ecosystems – also
show damage including reductions in growth (50%) arising from extreme winter warming events (Bjerke et al. 2011). Mosses, however, are not a food source for the autumnal moth (Jepsen et al. 2008) and so are likely to show differential responses to shrubs should climatic and herbivore outbreak events occur concurrently. Lichens were not affected by the extreme winter warming events and are not known to be grazed upon by the caterpillars. Therefore, lichens may benefit the most from extreme winter events and herbivore outbreaks. This contrasts sharply with the negative response observed in many summer warming studies (Cornelissen et al. 2001).

Belowground, soil frost following winter warming events reduces micro-arthropod abundance and changes their community composition (Bokhorst et al. 2012b) as species differ in cold tolerance. In addition, the negative effects of frost damage to dominant dwarf shrubs and mosses will also affect the micro-arthropod community (Salmane and Brumelis 2008; Bokhorst et al. 2014). Changes in plant and soil fauna community composition affects the carbon balance of an ecosystem as different plant functional types differ in their carbon sequestration rates and the decomposability of their litter (Cornelissen 1996; Bokhorst et al. 2007; De Deyn et al. 2008; Lang et al. 2009), while shifts in soil fauna community composition drive decomposition rates (Heemsbergen et al. 2004; Handa et al. 2014). In addition, shifts in the soil biota as a result of repeated extreme events can influence plant competition (Meisner et al. 2013). Therefore, changes in the soil and plant community as a result of these extreme events are likely to impact on the carbon balance of these sub-Arctic ecosystems. The direction of such changes is less clear as a previous autumnal moth outbreak in the Abisko area during 2004 reduced the CO₂ sink strength of the birch forest by 89% (Heliasz et al. 2011), while a moth outbreak in a Siberian taiga caused increases in CO₂ release from the soil due to the qualitative changes in the litter composition (Baranchikov et al. 2002). Thus, it is unclear what the combined effects of extreme weather events and herbivore peaks will be for the carbon balance of these sub-
Arctic ecosystems. By comparing the impacts of climatic and biotic events within one study system we are able to identify potential synergistic and antagonistic interactions between these events for ecosystem change. This may provide a better understanding of the driving factors behind long-term trends and spatial heterogeneity in sub-Arctic heath communities.

We studied the response of the above- and belowground communities to the multiple stresses of extreme winter warming and autumnal moth outbreaks to improve our understanding on how sub-Arctic ecosystems respond to multiple and interacting stress events. We expect that 1) the impact of moth grazing will increase the damage to plants previously exposed to extreme winter warming events. However, this effect will be plant-type-specific, and therefore we expect that: 2) dwarf shrubs will decline following the combined effects of winter warming events and moth defoliation and that graminoids will become dominant as the competition by the dwarf shrubs will be greatly reduced. 3) Cryptogams will benefit from the high vascular plant mortality as shading will be reduced (Bonan and Korzuhin 1989; van der Wal et al. 2005), and because cryptogams are not targeted by the autumnal moth (Jepsen et al. 2008). 4) Soil micro-arthropods will respond most strongly to the temperature extremes of the winter event while micro-arthropod responses to vegetation shifts will be more subtle. 5) As a result of the extreme winter warming events, CO₂ efflux during the following growing season will be negative for the ecosystem (net carbon source) due to high plant mortality, and this will be exacerbated by the occurrence of the autumnal moth grazing. However, declines in soil micro-arthropods, may limit CO₂ loss from the ecosystem, potentially leading to no net-effect on the CO₂ efflux rates.

Materials and Methods

Field site and experimental simulations
Simulations of winter warming events in the field were performed on a sub-Arctic heathland in open mountain birch forest close to the Abisko Scientific Research Station (ANS) in northern Sweden (68° 21' N, 18° 49' E) during March 2007, 2008 and 2009. Details of the research site and experimental set-up are described in Bokhorst et al. (2008; 2010). In brief, the experiment consisted of 18 plots (2.1 m × 1.0 m), consisting of 6 control plots (Cn) that remained under their natural snow cover throughout the winter, 6 that were exposed to a week-long winter warming event called canopy warming (CW) using infrared heating lamps (800 W emitting at 3 μm; HS 2408, Kalglo Electronics Co., Bethlehem, USA), and 6 where warming from infrared heating lamps was combined with soil warming from cables at 5 cm soil depth called canopy and soil warming (CSW). Soil warming cables (LS-TXLP, Nexans, Norway, producing 120 W m⁻²) were switched on two days after the lamps to simulate the delay in soil thaw during a real event. Temperatures were monitored with thermistors placed in each plot at canopy height and at the soil surface, with logging at 6-h intervals recorded on a data logger (CR10 X, Campbell Scientific, UK). Details on the temperature effects of the treatment are provided in Bokhorst et al. (2011; 2012b); in summary, temperatures rose on average to 5 °C during the events, while for the remainder of winter temperatures fluctuated in tandem with the ambient conditions (ranging from −17 °C to 4 °C) due to the diminished snow cover meaning there was no insulation from air temperatures. In contrast, control plots remained well insulated under snow and experienced temperatures between −7 °C and 0 °C until snowmelt. The simulation of extreme winter warming events and ecosystem responses were supported by observations of very similar impacts arising from a natural extreme event in the same region (Bokhorst et al. 2009).

Autumnal moth densities
The autumnal moth typically reaches population peaks approximately every 10 years (Tenow et al. 2004) with the Abisko outbreak of the moth caterpillars occurring during the 2012 and 2013 spring. The 2012 outbreak coincided with a very cool first half of the growing season, which caused a strong delay in plant phenology (Bjerke et al. 2014). Hence, birch leaf biomass was low by the start of the outbreak, and this probably accentuated the grazing pressure on understory plants since the caterpillars drop down onto the understory following consumption of the tree leaf resource. Vole and lemming population peaks also occurred in the Abisko region during the summers of 2010 and 2011 (Olofsson et al. 2013). However, there were no indications of grazing on any of the plants by these herbivores during those years, indicating that our study site was not visited by lemming and vole in sufficient numbers to affect the vegetation.

**Vegetation composition, shoot mortality and reproductive output**

Vegetation surveys were made by point quadrat measurements in permanent, randomly assigned squares (30 cm × 30 cm) in each plot of the winter warming experiment during mid-July (peak biomass) each year (2007-2013, except 2011). These surveys were therefore in the summers after the second and third winters of warming events and in the 4 subsequent summers (summers following winters with no simulated warming events). 121 point counts at 2.5 cm intervals were made of the vegetation in each square by counting the number of times a vertical pin touched plant parts. Cryptogam species were counted as present or absent, while vascular plants could be hit more than once by each vertical pin. For *E. nigrum*, only shoots were counted rather than every leaf hit to avoid over-representation due to the high number of tightly packed needle-like leaves. Correlations between point quadrat hits and biomass were made for the dominant study species on quadrats outside the experimental plots by quantifying hits in the same way and afterwards harvesting all aboveground parts. These correlations were used to quantify species biomass in each experimental plot (Jonasson 1988). Species cover was
quantiﬁed from point count surveys based on presence or absence at each point. Shannon diversity index (H’) was quantiﬁed as a measure of plant diversity for each plot using the point intercept data.

Shoot mortality of three dominant dwarf shrub species (E. nigrum, V. myrtillus and V. vitis-idaea) was quantiﬁed by counting the number of dead and alive shoots in a randomly assigned 30 cm × 30 cm quadrat in each plot during mid-June every year from 2008 to 2013 (except 2011 when a survey was not undertaken). A shoot was considered dead when all leaves on its stem were brown and had died. A berry count was done during July 2013 by quantifying the number of shoots with berries for each of the three dwarf shrub species in a 1 m × 1 m quadrat in each plot.

Micro-arthropod community composition

To monitor the abundance and diversity of soil micro-arthropods, an intact soil core (10 cm diameter, 5 cm long) was sampled from each experimental plot as soon as the ﬁrst 5 cm of soil had thawed in spring, which generally occurred in early May. Sampling was done following the third extreme winter warming simulation in 2009 and after three years without events (2012). Samples were individually stored in sealed plastic containers and kept at 5 ºC until extracted from the core in a Tullgren heat extractor (Van Straalen and Rijninks 1982) for three weeks. Extracted arthropods were preserved in alcohol (70 % ethanol). Collembola were identiﬁed to species level following Fjellberg (1998; 2007). Acari were determined to family level following Karg (1993), Krantz and Walter (2009) and Weigmann (2006), with the exception of the Prostigmata and Astigmata which were grouped together. The Shannon Diversity Index (H’) was quantiﬁed as a measure of Collembola species diversity and at the family level for the Acari (also including higher taxonomic levels). Collembola species were grouped according to their typical association with the different soil layers. As such, there were
eu-edaphic species that tend to live deeper in the soil, hemi-edaphic species that live in the litter layer and epi-edaphic species living among the aboveground parts of plants (Gisin 1943). Collemboila size tends to decrease further down the soil profile. This information was not available for the studied Acari in this study.

**Ecosystem CO2 fluxes**

Ecosystem CO2 fluxes were measured once during the growing seasons (mid-July) of 2012 and 2013 in the same was as previously done in these experimental plots (Bokhorst et al. 2011). Measurements were made by placing a transparent chamber (20 cm × 20 cm × 20 cm) made from polymethyl methacrylate (PMMA) over the vegetation and by quantifying CO2 change using an Infrared Gas Analyzer (EGM-4, PP-systems, Amesbury, MA, USA). Net Primary Production (NPP) was quantified by monitoring the rate of change in the headspace CO2 concentration at 10 second intervals over a 3 minute period while Ecosystem Respiration (ER) was quantified by darkening the chamber with black plastic sheeting. The difference between ER and NPP determined Gross Primary Production (GPP). To minimize internal chamber air exchange with the external environment, plastic skirts (20 cm wide) weighed down with chains were attached to a square frame, onto which the chamber could be attached (Street et al. 2007). An internal fan was used to mix air inside the chamber. Photosynthetic Active Radiation (PAR) was measured (SKP 215 Skye Instruments, Powys, UK) at the start and end of each measurement and was on average 1000 µmol m−2 s−1.

**Data and statistical analyses**

Repeated measures ANOVA were used to identify changes across years and between treatments for species richness, diversity (H’), plant biomass (individual species, evergreen biomass, deciduous biomass, dwarfs shrubs and (hemi) cryptophytes), cryptogam cover and the ratio of alive-to-dead shoot counts of *E. nigrum*, *V. myrtillus* and *V. vitis-idaea*. Plant reproductive
output and CO₂ efflux rates were compared across treatment plots using one-way ANOVAs. Micro-arthropod responses to the winter warming events were determined with one-way ANOVA on species abundance, total Collembola and Acari abundance, species richness, and diversity (H’). In all cases, homogeneity of variance was tested with a Levene’s test of equality and log-transformation was applied when necessary. All statistical analyses were done using SPSS 22.0 (IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY).

Results

Vascular plant damage from climatic and biotic events

The extreme winter warming events resulted in considerable shoot mortality of *E. nigrum*, *V. vitis-idaea* and *V. myrtillus* (Table 1, Fig. 1). Shoot damage remained high for *E. nigrum* and *V. vitis-idaea* in the Cn and CSW plots during the following years except *V. myrtillus* which showed a rapid recovery in 2010 (Fig. 1c). Following the autumnal moth peak of 2013 all three dwarf shrubs had high shoot mortality but now also in the Cn plots. In addition, there were no berries on *V. myrtillus* and *V. vitis-idaea* in any of the plots during 2013 after the moth outbreak, while *E. nigrum* had on average 1.5 (±1.1 SE), 0.5 (±0.2) and 0.3 (±0.1) berries per shoot for Cn, CW and CSW respectively.

Plant functional type and growth form responses to climatic and biotic events

Total deciduous shrub biomass increased (25 %) in the extreme winter warming treated plots compared to the starting conditions of 2007 and remained higher irrespective of the autumnal moth peaks (Fig. 2a). However, deciduous shrub biomass in the control plots showed a decreasing trend with time from 2007 but a large biomass decline between 2012 and 2013 (the moth outbreak years) and was different (F₂,₁₅ = 5.0, *P* < 0.022) from that of CSW during 2013. *Vaccinium myrtillus* biomass decreased in all plots in 2013 compared to the previous year (Fig. 2b), while there was no consistent pattern for the biomass of *V. uliginosum* across the treatments.
Deschampsia flexuosa increased with time irrespective of treatments (Fig. 2d). Mean species biomasses across plots for each year are presented in S1.

Total evergreen shrub biomass declined following the extreme winter warming treatments (Fig. 2e), but increased to the initial values of 2007 by 2012. In 2013, following the autumnal moth peak, biomass decreased again, but on this occasion also in the control plots, similar to the decreases observed in treated plots following the extreme winter warming events (Fig. 2e). These biomass changes were driven by the mortality of *E. nigrum* (Figs 1d and 2f), as no consistent changes were observed in *V. vitis-idaea* (Table 1, Fig. 2g). However, biomass of *Linnea borealis* (a much smaller component of the vegetation) increased with time reaching highest biomass change across all treatments in 2013 (Table 1, Fig. 2h, S1). The biomass of dwarf shrubs showed the same pattern as found for evergreen plants across the study period (Table 2, data not shown) since evergreens contribute the most to dwarf shrub biomass. Change in biomass of (hemi)cryptophytes increased over time showing the same pattern as *D. flexuosa* and *L. borealis* (Table 1).

Vascular plant diversity (*H’*) did not differ between the treatment plots during any of the years, and neither was there a consistent pattern in diversity across years despite the significant year effect (Table 2). Species richness gradually increased with time; from 4.5 during 2007 to 5.1 in 2013, but no differences were found between the experimental plots (Table 2). This species richness increase was mostly driven by the appearance of grasses (*Calamagrostis lapponica* and *D. flexuosa*) where they were previously absent.

**Cryptogam community changes following climatic and biotic events**

Total moss (mostly *Hylocomium splendens*) and lichen cover increased, irrespective of treatments (Table 1), following the autumnal moth peaks (2012 and 2013) (Fig. 3). There were no treatment effects on cryptogam community species richness or diversity (H’) during any of
the years but cryptogam richness increased \((P < 0.001)\) from on average 2 species per plot to 4 in 2012 and 2013 following the moth outbreak. Similarly, diversity \((H')\) increased \((P < 0.001)\) from 0.4 (mean of 2007-2010) to 1.0 during 2012 and 2013. The increased species richness and diversity \((H')\) were driven by the emergence of *Cladonia rangifera*, *Nephroma arcticum*, *Ptilium ciliare* and *Dicranum* sp. in plots where these were previously not observed.

**Micro-arthropod responses to climatic and biotic events**

Abundance of Collembola was significantly reduced (46%) in CSW following the third winter warming simulation event compared to control plots (Table 3). Changes in Collembola abundance were primarily the result of declines (45%) in soil-dwelling species (*Isotomiella minor* 57%). In 2012 total Collembola abundance was no longer different between treatments but surface-dwelling species abundance (notably *Lepidocyrtus lignorum*) was reduced by 70% \((P < 0.05)\) in CSW compared to Cn (Table 3). Total Acari abundance was reduced in the CW and CSW treatments by 41% and 48%, respectively compared to the control plots in 2009 (Table 3). These changes were driven by declines (43% and 49%, respectively) in Astigmata-Prostigmata and a 31% and 50% decline in total Mesostigmata and Oribatida respectively in CSW. None of the individual Oribatida families were affected by the extreme winter warming events, and in 2012, no differences were found for the total Acari and any group abundances between treatments.

There were no diversity \((H')\) or richness differences for the Collembola between the treatments and control plots during 2009 and 2012, except for a difference \((F_{2,15} = 5.5, P = 0.016)\) between CW \((H': 1.3 \pm 0.1)\) and CSW \((H': 1.6 \pm 0.05)\) in 2009. Diversity \((H')\) of Acari was higher \((F_{2,15} = 4.4, P = 0.032)\) in CW \((1.3 \pm 0.02)\) compared to Cn \((1.1 \pm 0.03)\) in 2009 and driven by changes in relative abundance. No Acari diversity \((H')\) differences were found in 2012.

\(CO_2\) efflux
ER and GPP were lower in CSW (58 % and 95 % respectively) compared to Cn in 2009 while there were no differences in ER and GPP between the experimental treatment plots during 2012 and 2013, (Table 4, S3). NPP was consistently lower in Cn compared to CSW across all years.

**Discussion**

Extreme climatic events and population outbreaks of herbivores are well known drivers of community change but these are rarely compared within one experimental study as shown here (Callaghan et al. 2013). There were clear responses to the climatic and biotic events and these were often species or functional group specific. As such, evergreen dwarf shrubs were negatively affected by both extreme winter warming events and moth grazing. The deciduous dwarf shrub *V. myrtillus* was only affected by the autumnal moths, in control plots, without previous exposure to winter warming events, indicating that some vegetation changes in sub-Arctic regions may depend on the history of past extreme events. Cryptogams increased during the 7 year period without major responses to the treatments. Furthermore, micro-arthropod response to extreme winter warming events was strongest among the eu-edaphic and smaller invertebrate species. In contrast, resulting shifts in the plant community composition hardly affected the soil micro-arthropod community (no response following herbivory). These different responses suggest that soil micro-arthropods respond immediately to temperature variability during winter and that changes in the plant community have much less impact in these sub-Arctic ecosystems.

We did not observe, as hypothesised, increased additional damage to dwarf shrubs by the autumnal moth grazing following the extreme winter warming events. Although the damage of the moth caterpillar grazing and the extreme winter warming events were similar in extent, for *E. nigrum*, the period between the events (3 years) seems long enough such that there were no synergistic impacts of both events on the plants. However, the decline of the deciduous *V.*
following the moth caterpillars in 2013 was, however, not consistent across experimental plots: more damage was found in the control and CW treatment, while no apparent increase in shoot mortality was observed in the CSW plots, indicating that the moth caterpillars may have avoided eating from the plants in the CSW treatment. This apparent reduced feeding on *V. myrtillus* may reflect increased concentration of phenolic defence compounds or reduced nutrient availability (Herms and Mattson 1992; Awmack and Leather 2002). The damage to plants caused by extreme winter warming events is largely dependent on snow thickness (Bokhorst *et al.* 2009), which is driven by local topography and wind direction, whereas the damage caused by herbivore peaks depends on their spatial distribution across the landscape. Potentially synergistic or antagonistic effects of climatic and biotic events on vegetation change are therefore not equally distributed across the landscape, but may play a role in the spatial distribution and heterogeneity of plant communities and their response to gradual climate warming. Overall, evergreen dwarf shrubs appear the most susceptible to extreme events and therefore may experience more abiotic stress and competition than deciduous shrubs during future climate change.

We did not find support for our second hypothesis that the decline of dwarf shrubs would enable graminoids to dominate. The lack of response by the graminoids may be due to the afterlife effects of *E. nigrum* litter which contains high concentrations of secondary compounds that inhibits growth of other plants (Nilsson and Zackrisson 1992; Gallet *et al.* 1999; Wallstedt *et al.* 2000). However, *D. flexuosa* (and *L. borealis*) increased with time irrespective of extreme winter warming treatments or biomass of *E. nigrum*, suggesting that in 2010, other factors such as climatic conditions for growth had improved in combination with increased opening of micro-sites (Nathan and Muller-Landau 2000). Overall, our results indicate that graminoids and (hemi)cryptophytes are less affected by extreme climatic and biotic events than other plant functional types. Their growth strategy, with dormant buds remaining at ground level, probably
protects them against grazing and pre-mature winter de-hardening. However, repeated extreme events are probably required before the dominance of *E. nigrum* is broken in these sub-Arctic heathland ecosystems.

Mosses and lichens increased in cover following damage caused to dwarf shrubs supporting our third hypothesis. Critically, this increase manifested itself across all experimental plots and appears largely in response to the autumnal moth grazing. While highlighting the importance of the moth outbreak in causing major increases in the plants, it also shows that the winter warming events did not allow increased cryptogam growth in contrast to what was expected. This lack of warming event response potentially reflects the reduced growth rates (50 %) immediately following these climatic events for the dominant bryophyte *H. splendens* (Bjerke *et al*. 2011). Furthermore, the cryptogams increased despite a recovery of the dwarf shrubs between 2009 and 2012, suggesting that conditions were suitable for cryptogam growth and that there was little competition, in terms of canopy opening and light for space (Keuper *et al*. 2011). The overall increased growth of cryptogams may have been promoted by higher precipitation during summer months (Tamm 1964; Vitt 1990; Potter *et al*. 1995; Sonesson *et al*. 2002). Precipitation recorded at the ANS research station was higher during the summers of 2011 and 2012 (37 % and 17 %, respectively) than previous years (2007-2010) and the long-term mean (1913-2000). In addition, there would have been no grazing pressure on the cryptogams by the autumnal moths. Instead, there would have been an increase in nutrients from caterpillar faecal matter (Karlsen *et al*. 2013) that may have contributed to increased moss growth (Aerts *et al*. 1992; Armitage *et al*. 2012). Therefore, the observed increase of cryptogams most likely reflects a response to the wetter summers and the autumnal moth peak increasing nutrient availability, reducing competition from vascular plants and increased light through the damaged canopy.
In support of hypothesis four we found that the micro-arthropod community was more responsive to extreme climatic events than changes in the plant community, which is consistent with soil micro-arthropods responses to extreme climatic disturbances (Coulson et al. 2000; Bokhorst et al. 2012b). The lack of response by micro-arthropods to changes in the plant community is consistent with a study from a northern boreal forest (Bokhorst et al. 2014) but is inconsistent with findings from temperate grasslands (Wardle et al. 1999; 2005). A potential explanation between these contrasting responses lays with the quality of the soil carbon pool which is much lower and has a much slower turnover rate in northern boreal and sub-Arctic ecosystems, as compared to temperate grasslands (Carvalhais et al. 2014). Effects of changes in the plant community on the soil organic matter layer will therefore take years or decades before they impact on the soil micro-arthropod community and vice-versa (Hågvar 1984; Salmon et al. 2006; Bokhorst et al. 2014). In addition, the micro-arthropods in these sub-arctic ecosystems may have enough feeding plasticity that the changes in food supply and quality do not affect them overly much (Siepel and De Ruiter-Dijkman 1993; Krab et al. 2013). Our results indicate that soil micro-arthropod community changes as a result of extreme climate events tends to be rapid but that recovery is also quick. However, during these recovery periods the shift in soil fauna community composition may feed-back to soil carbon cycling rates (Heemsbergen, 2004 #1198; Handa, 2014 #3609).

The measured declines in ER and GPP coincided with declines of Collembola and Acari abundance in the experimental plots during 2009 and may be linked but these changes in ER and GPP also coincided with high plant mortality and did not seem to extend beyond that specific growing season. The CO2 fluxes measured during 2012 and 2013 were particularly low compared to reported measurements in this region (Larsen et al. 2007) but close to zero gas fluxes have been reported previously (Lafleur et al. 2003) so this may not be unusual. A continuous measuring campaign across the growing season may have shown a different pattern
between the experimental plots but as it is the overall consistent low measured gas flux rate
probably reflect the massive defoliation caused by the autumnal moth (Heliasz et al. 2011; Medvigy et al. 2012; Simmons et al. 2014). Therefore, we did not find consistent support for hypothesis five.

Overall, these results support the notion that the response of sub-Arctic ecosystems in response to the pressures of climate change is non-linear (Callaghan et al. 2010; 2013). Extreme events will (at least temporarily) halt or push vegetation change away from the general ‘greening’ trends driven by summer warming, but will also interact with sudden population explosions of herbivores leading to steep changes in vegetation composition (Fig. 4). Based on current evidence, it seems that evergreen dwarf shrubs appear most sensitive to extreme climatic events and grazing pressure, indicating that there is a cost associated with being evergreen in a future climate with more extreme events. Even though these E. nigrum heathlands are very resistant to change (Aerts 2010) future community changes are likely given the increased frequencies of extreme events expected due to climate change (Callaghan et al. 2010; AMAP 2011). Therefore, these sub-Arctic heath communities may shift from an evergreen and moss dominated vegetation to one dominated by deciduous dwarf shrubs and graminoids. Such changes will likely result in altered soil communities and may initiate decomposition of stored soil carbon turning these ecosystems into a net source of carbon due to the higher carbon turnover rates in these latter vegetation types (De Deyn et al. 2008; Hartley et al. 2012). Taken together, these results indicate that vegetation and soil community changes in the sub-Arctic are currently unpredictable and will be highly variable across the landscape.

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This research was supported by the Research Council of Norway (contract nos. 171542/V10, 216434/E10 and 225006/E10), a Leverhulme Trust (UK) grant awarded to G.K.P. and T.V.C. (grant F/00118/AV), by ATANS grants (EU Transnational Access Programme, FP6 Contract no. 506004) to S.B., J.W.B. and G.K.P, and by FRAM – High North Research Centre for Climate and Environment through its terrestrial flagship programme. Infrastructure and equipment support was supplied by the Royal Swedish Academy of Sciences and by Frank Bowles and Jerry Melillo from the Marine Biological Laboratory in Woods Hole, MA, USA, who also contributed to the experimental design and instrumentation. T.V.C. was further supported by FORMAS (214-2008-188) and the EU Framework 7 Infrastructure Project “INTERACT” (www.eu-interact.com).

References:


Tables

Table 1. Repeated measures ANOVA statistics (F and P values) of alive:dead shoot ratios, plant functional types and species-specific biomass and cryptogam cover in the experimental winter warming event plots. N = 6 for each treatment (control, canopy warming and canopy and soil warming). Vegetation surveys were conducted each year from 2007 to 2013 except during 2011. Ds = dwarf shrub; hemicyryptophytes include: *L. borealis* and grasses.

| Table 1. Repeated measures ANOVA statistics (F and P values) of alive:dead shoot ratios, plant functional types and species-specific biomass and cryptogam cover in the experimental winter warming event plots. N = 6 for each treatment (control, canopy warming and canopy and soil warming). Vegetation surveys were conducted each year from 2007 to 2013 except during 2011. Ds = dwarf shrub; hemicyryptophytes include: *L. borealis* and grasses. |
|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|
| **Treatment**                                   | **Year**                                        | **T × Y**                                       |
| **F (2,15)**                                    | **P**                                           | **F (4,60)**                                    | **P**                                           | **F (8,60)**                                    | **P**                                           |
| Alive:dead shoots                              |                                                 |                                                 |                                                 |                                                 |                                                 |
| *E. nigrum*                                     | 13.8                                            | 0.001                                          | 0.7                                             | 0.596                                          | 2.0                                             | 0.128                                          |
| *V. vitis-idaea*                                | 52.6                                            | <0.001                                         | 1.8                                             | 0.171                                          | 1.8                                             | 0.144                                          |
| *V. myrtillus*                                  | 10.7                                            | 0.002                                          | 9.7                                             | <0.001                                         | 3.3                                             | 0.004                                          |
| Biomass                                         |                                                 |                                                 |                                                 |                                                 |                                                 |                                                 |
| Deciduous                                       | 2.8                                             | 0.094                                          | 4.0                                             | **0.006**                                      | 2.3                                             | 0.033                                          |
| *V. myrtillus* (ds)                             | 2.1                                             | 0.152                                          | 14.9                                            | <0.001                                         | 2.4                                             | **0.028**                                      |
| *V. uliginosum* (ds)                            | 0.9                                             | 0.414                                          | 0.5                                             | 0.593                                          | 2.3                                             | 0.092                                          |
| *D. flexuosa*                                   | 0.4                                             | 0.666                                          | 7.7                                             | **0.001**                                      | 0.4                                             | 0.826                                          |
| Evergreens                                      | 0.9                                             | 0.422                                          | 5.1                                             | **0.010**                                      | 3.0                                             | **0.029**                                      |
| *E. nigrum* (ds)                                | 0.9                                             | 0.426                                          | 9.9                                             | <0.001                                         | 2.7                                             | **0.036**                                      |
| *V. vitis-idaea* (ds)                           | 0.7                                             | 0.510                                          | 2.1                                             | 0.122                                          | 0.5                                             | 0.797                                          |
| *L. borealis*                                   | 0.8                                             | 0.449                                          | 6.4                                             | **0.006**                                      | 0.8                                             | 0.521                                          |
| Dwarf shrubs                                    | 0.9                                             | 0.427                                          | 7.3                                             | <0.001                                         | 3.8                                             | **0.004**                                      |
| Hemicryptophytes                                | 0.7                                             | 0.526                                          | 11.1                                            | <0.001                                         | 0.8                                             | 0.537                                          |
| Moss (% cover)                                  | 0.8                                             | 0.459                                          | 8.0                                             | **0.001**                                      | 0.8                                             | 0.549                                          |
| Lichen (% cover)                                | 1.6                                             | 0.424                                          | 50.8                                            | <0.001                                         | 0.9                                             | 0.464                                          |
Table 2. Repeated measures ANOVA statistics (F and P values) of the plant and cryptogam diversity (H') and species richness in the plots of the extreme winter warming event simulations. The experiment included 3 treatments of 6 replicate plots each and vegetation surveys were conducted each year from 2007 to 2013 except during 2011.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Year</th>
<th>T × Y</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F (2,15)</td>
<td>P</td>
</tr>
<tr>
<td>Vascular plants</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diversity (H')</td>
<td>0.8</td>
<td>0.467</td>
</tr>
<tr>
<td>Richness</td>
<td>0.0</td>
<td>0.983</td>
</tr>
<tr>
<td>Cryptogams</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diversity (H')</td>
<td>1.6</td>
<td>0.237</td>
</tr>
<tr>
<td>Richness</td>
<td>1.9</td>
<td>0.188</td>
</tr>
</tbody>
</table>
Table 3. Collembola species and Acari group abundance (ind. × 1000 / m²) in the extreme winter warming event plots. 2009 data sampled following the third winter warming simulation and the 2012 data represent sampling after three years without treatments. Data are mean of n = 6 with standard error between parentheses. Significant differences (Tukey HSD $P < 0.05$) between treatments are indicated by different letters. Cn: control, CW: canopy warming, CSW: Canopy and soil warming. Eu-edaphic: living in the soil, hemi-edaphic: living among the litter layers, epi-edaphic: living among the plant canopy.

<table>
<thead>
<tr>
<th>Species</th>
<th>2009</th>
<th></th>
<th></th>
<th>2012</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cn</td>
<td>CW</td>
<td>CSW</td>
<td>Cn</td>
<td>CW</td>
<td>CSW</td>
</tr>
<tr>
<td><em>Lepidocyrtus lignorum</em></td>
<td>1.38 (0.024)</td>
<td>1.06 (0.044)</td>
<td>1.08 (0.28)</td>
<td>2.53 (0.50)ab</td>
<td>1.40 (0.48)ab</td>
<td>0.68 (0.13)b</td>
</tr>
<tr>
<td><em>Entomobrya nivalis</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Dicrtrömina fusca</em></td>
<td>0.02 (0.02)</td>
<td>0.06 (0.04)</td>
<td>0.17 (0.08)</td>
<td>0.76 (0.35)</td>
<td>0.34 (0.13)</td>
<td>0.30 (0.11)</td>
</tr>
<tr>
<td></td>
<td>epi</td>
<td>edaphic</td>
<td>1.40 (0.23)</td>
<td>1.12 (0.44)</td>
<td>1.25 (0.34)</td>
<td>3.35 (0.84)ab</td>
</tr>
<tr>
<td><em>Pseudachorutus corticicolus</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.19 (0.05)</td>
</tr>
<tr>
<td><em>Folsomia quadrioculata</em></td>
<td>4.22 (1.41)</td>
<td>2.14 (0.60)</td>
<td>1.51 (0.39)</td>
<td>1.42 (0.37)</td>
<td>2.42 (0.65)</td>
<td>2.59 (1.18)</td>
</tr>
<tr>
<td><em>Parisotoma notabilis</em></td>
<td>0.06 (0.04)</td>
<td>0</td>
<td>0</td>
<td>0.40 (0.14)</td>
<td>0.19 (0.09)</td>
<td>0.11 (0.05)</td>
</tr>
<tr>
<td><em>Isotoma viridis</em></td>
<td>0.06 (0.04)</td>
<td>0</td>
<td>0.11 (0.05)</td>
<td>0.06 (0.03)</td>
<td>0.28 (0.07)</td>
<td>0.13 (0.07)</td>
</tr>
<tr>
<td><em>Isotoma riparia</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>0.06 (0.04)</td>
<td>0.02 (0.02)</td>
</tr>
<tr>
<td><em>Isotoma sp./Isotomurus sp.</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.36 (0.09)</td>
<td>0.28 (0.04)</td>
<td>0.23 (0.04)</td>
</tr>
<tr>
<td><em>Desoria sp.</em></td>
<td>0.28 (0.12)</td>
<td>0.30 (0.10)</td>
<td>0.15 (0.05)</td>
<td>0</td>
<td>0.02 (0.02)</td>
<td>0.02 (0.02)</td>
</tr>
<tr>
<td></td>
<td>hemi</td>
<td>edaphic</td>
<td>4.63 (1.46)</td>
<td>2.44 (0.64)</td>
<td>1.76 (0.41)</td>
<td>2.44 (0.37)</td>
</tr>
<tr>
<td><em>Protaphorura cf. gisini</em></td>
<td>2.84 (0.51)</td>
<td>2.16 (0.67)</td>
<td>3.71 (0.47)</td>
<td>3.54 (0.87)</td>
<td>2.33 (0.48)</td>
<td>3.65 (1.05)</td>
</tr>
<tr>
<td><em>Willemia anophtalma</em></td>
<td>5.16 (1.93)</td>
<td>5.18 (2.78)</td>
<td>2.19 (0.43)</td>
<td>1.42 (0.79)</td>
<td>1.90 (0.94)</td>
<td>0.81 (0.23)</td>
</tr>
<tr>
<td><em>Folsomia sensibilis</em></td>
<td>0.28 (0.25)</td>
<td>0</td>
<td>0.49 (0.33)</td>
<td>1.80 (1.12)</td>
<td>0.59 (0.35)</td>
<td>0.87 (0.71)</td>
</tr>
<tr>
<td><em>Paramura sexpunctata</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.04 (0.04)</td>
<td>0</td>
<td>0.02 (0.02)</td>
</tr>
<tr>
<td><em>Isotomiella minor</em></td>
<td>15.00 (2.00)a</td>
<td>9.46 (1.73)ab</td>
<td>6.41 (1.56)ab</td>
<td>1.68 (0.40)</td>
<td>1.87 (0.71)</td>
<td>0.81 (0.23)</td>
</tr>
<tr>
<td><em>Megalothenax minimus</em></td>
<td>0.25 (0.14)</td>
<td>0.13 (0.07)</td>
<td>0.25 (0.08)</td>
<td>0.02 (0.02)</td>
<td>0.06 (0.02)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>eu</td>
<td>edaphic</td>
<td>23.53 (2.34)a</td>
<td>16.93 (3.65)ab</td>
<td>13.05 (1.66)ab</td>
<td>8.51 (2.69)</td>
</tr>
<tr>
<td><strong>Collembola total</strong></td>
<td>29.56 (1.76)a</td>
<td>20.50 (3.18)ab</td>
<td>16.06 (2.08)ab</td>
<td>14.30 (2.74)</td>
<td>11.86 (1.58)</td>
<td>10.36 (2.51)</td>
</tr>
<tr>
<td><strong>Oribatida</strong></td>
<td>68.0 (13.5)a</td>
<td>38.3 (3.0)ab</td>
<td>34.3 (7.1)ab</td>
<td>68.8 (11.7)</td>
<td>51.7 (8.0)</td>
<td>54.2 (8.1)</td>
</tr>
<tr>
<td><strong>Astigmata-Prostigmata</strong></td>
<td>65.3 (5.6)a</td>
<td>37.2 (3.9)ab</td>
<td>33.2 (4.4)ab</td>
<td>22.0 (5.4)</td>
<td>46.6 (13.6)</td>
<td>25.6 (5.1)</td>
</tr>
<tr>
<td><strong>Mesostigmata</strong></td>
<td>10.2 (0.9)a</td>
<td>9.2 (0.9)ab</td>
<td>7.1 (0.9)ab</td>
<td>9.5 (2.2)</td>
<td>6.5 (1.4)</td>
<td>6.9 (0.8)</td>
</tr>
<tr>
<td><strong>Acari total</strong></td>
<td>143.5 (15.7)a</td>
<td>84.7 (4.9)ab</td>
<td>74.5 (8.9)ab</td>
<td>100.3 (16.4)</td>
<td>104.8 (12.9)</td>
<td>86.6 (7.7)</td>
</tr>
</tbody>
</table>
Table 4. Repeated measures ANOVA statistics (F and P values) of the ecosystem gas flux (CO₂) measurements during 2009, 2012 and 2013. The experiment included 3 treatments of 6 replicate plots each.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Year F (2,15)</th>
<th>Year P</th>
<th>T × Y F (2,30)</th>
<th>T × Y P</th>
</tr>
</thead>
<tbody>
<tr>
<td>ER</td>
<td>3.2</td>
<td>0.070</td>
<td>40.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NPP</td>
<td>4.1</td>
<td>0.027</td>
<td>38.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>GPP</td>
<td>4.8</td>
<td>0.025</td>
<td>5.9</td>
<td>0.007</td>
</tr>
</tbody>
</table>
Figures

Figure 1. Shoot damage to the dominant dwarf shrub species in the extreme winter warming plots and from subsequent autumnal moth outbreak. Alive:dead shoot ratios of *E. nigrum* (a), *V. vitis-idaea* (b) and *V. myrtillus* (c). Grey shaded area indicates years with extreme winter warming event simulations and the vertical dashed line indicates the start of the autumnal moth outbreak (2012 and 2013). Cn: control, CW: Canopy warming, CSW: Canopy and soil warming. Bars are mean of 6 replicate plots with SE as error bars. ANOVA statistics are shown in Table 1. Data up to 2009 were previously presented in Bokhorst et al. (2011).

Figure 2. Change in total deciduous and evergreen plant biomass and individual species following extreme winter warming events and autumnal moth outbreaks. The percentage changes are in relation to the recorded biomass of 2007. Grey shaded area indicates period with extreme winter warming events and the vertical dashed line indicates the start of the autumnal moth peaks (2012 and 2013). Cn: control, CW: Canopy warming, CSW: Canopy and soil warming. Bars are mean of n = 6 replicate plots with SE as error bars. ANOVA statistics are shown in Table 2.

Figure 3. Changes in moss and lichen cover following extreme winter warming events (2007-2009) and the autumnal moth outbreaks (2012 and 2013). The percentage changes are in relation to the species cover measured in 2007. Cn: control, CW: Canopy warming, CSW: Canopy and soil warming. Bars are mean of n = 6 replicate plots with SE as error bars. ANOVA statistics are shown in Table 2.
Figure 1

(a) *E. nigrum*  
(b) *V. vitis-idaea*  
(c) *V. myrtillus*

Alive:dead shoots (ratio)

2008 2009 2010 2011 2012 2013
Figure 2

Deciduous

(a) total

(b) V. myrtillus

(c) V. uliginosum

(d) D. flexuosa

Evergreens

(e) total

(f) E. nigrum

(g) V. vitis-idaea

(h) L. borealis

Biomass change (%)

2008 2009 2010 2011 2012 2013
Figure 3.

(a) Mosses
(b) Lichens

Cover change (%)

2008 2009 2010 2011 2012 2013
Supporting information 1. Biomass of deciduous and evergreen plants following extreme winter warming events and an autumnal moth outbreak (2012 and 2013). Data points are means of \( n = 6 \) replicate plots with SE as error bars. Cn: control, CW: Canopy warming, CSW: Canopy and soil warming. ANOVA statistics for the % changes in biomass are shown in Table 2. Grey shaded areas indicate periods with extreme winter warming events. Vertical dashed line indicates the start of the autumnal moth peaks (2012 and 2013).
S2. Acari group and family abundance (ind. × 1000 / m²) in the extreme winter warming event plots. 2009 data sampled following the third winter warming simulation and the 2012 data represent sampling after three years without treatments. Data are mean of n = 6 with standard error between parentheses. Significant differences (Tukey HSD P < 0.05) between treatments are indicated by different letters. Cn: control, CW: canopy warming, CSW: Canopy and soil warming.

<table>
<thead>
<tr>
<th></th>
<th>2009</th>
<th></th>
<th></th>
<th>2012</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cn</td>
<td>CW</td>
<td>CSW</td>
<td>Cn</td>
<td>CW</td>
<td>CSW</td>
</tr>
<tr>
<td>Astigmata-Prostigmata</td>
<td>65.3 (5.6)a</td>
<td>37.2 (3.9)b</td>
<td>33.2 (4.4)b</td>
<td>22.0 (5.4)</td>
<td>46.6 (13.6)</td>
<td>25.6 (5.1)</td>
</tr>
<tr>
<td>Total Oribatida</td>
<td>68.0 (13.5)a</td>
<td>38.3 (3.0)ab</td>
<td>34.3 (7.1)b</td>
<td>68.8 (11.7)</td>
<td>51.7 (8.0)</td>
<td>54.2 (8.1)</td>
</tr>
<tr>
<td>Oppiidae</td>
<td>57.4 (14.1)</td>
<td>31.2 (2.2)</td>
<td>28.8 (7.0)</td>
<td>50.7 (11.2)</td>
<td>34.8 (5.5)</td>
<td>36.0 (7.7)</td>
</tr>
<tr>
<td>Phthiracaridae</td>
<td>0.2 (0.0)</td>
<td>0.3 (-)</td>
<td>0.1 (-)</td>
<td>0.0 (0.0)</td>
<td>0.1 (0.0)</td>
<td>0.2 (0.0)</td>
</tr>
<tr>
<td>Damaeus</td>
<td>0.3 (0.1)</td>
<td>0.2 (0.1)</td>
<td>0.1 (0.1)</td>
<td>0.3 (0.1)</td>
<td>0.1 (0.1)</td>
<td>0.2 (0.1)</td>
</tr>
<tr>
<td>Notrhidae</td>
<td>1.1 (0.3)</td>
<td>1.2 (0.3)</td>
<td>1.1 (0.4)</td>
<td>1.4 (0.6)</td>
<td>0.4 (0.1)</td>
<td>1.1 (0.3)</td>
</tr>
<tr>
<td>Brachypylina</td>
<td>9.4 (3.4)</td>
<td>6.0 (2.1)</td>
<td>4.3 (0.6)</td>
<td>15.2 (3.7)</td>
<td>15.1 (5.1)</td>
<td>15.2 (4.3)</td>
</tr>
<tr>
<td>Total Mesostigmata</td>
<td>10.2 (0.9)a</td>
<td>9.2 (0.9)ab</td>
<td>7.1 (0.9)b</td>
<td>9.5 (2.2)</td>
<td>6.5 (1.4)</td>
<td>6.9 (0.8)</td>
</tr>
<tr>
<td>Parasitidae</td>
<td>6.2 (0.6)</td>
<td>5.6 (1.0)</td>
<td>4.9 (0.4)</td>
<td>4.9 (1.2)</td>
<td>3.8 (0.6)</td>
<td>4.3 (0.4)</td>
</tr>
<tr>
<td>Trachytidae</td>
<td>0.9 (0.3)</td>
<td>0.9 (0.3)</td>
<td>0.3 (0.1)</td>
<td>1.5 (0.6)</td>
<td>0.9 (0.4)</td>
<td>0.5 (0.2)</td>
</tr>
<tr>
<td>Uropodidae</td>
<td>3.1 (0.5)</td>
<td>2.7 (0.6)</td>
<td>1.9 (0.6)</td>
<td>3.1 (0.7)</td>
<td>1.8 (0.5)</td>
<td>2.0 (0.3)</td>
</tr>
<tr>
<td>Total Acari</td>
<td>143.5 (15.7)a</td>
<td>84.7 (4.9)b</td>
<td>74.5 (8.9)b</td>
<td>100.3 (16.4)</td>
<td>104.8 (12.9)</td>
<td>86.6 (7.7)</td>
</tr>
</tbody>
</table>
S3. Ecosystem CO₂ flux rates of experimental plots during 2009, 2012 and 2013. The 2012 and 2013 flux rates were consistently lower compared to 2009 (see table 3 for ANOVA statistics).

Gross primary production (GPP) is the difference between CO₂ flux measurements in full ambient daylight (NPP) and ecosystem respiration (ER) measured in blacked-out chambers. Positive values indicate CO₂ flux from the system to the atmosphere and negative CO₂ flux from the atmosphere into the system. Bars with different letters indicate significant (Tukey’s HSD P < 0.05) differences between treatments. Bars are means of four to six replicate plots, error bars are SE. The 2009 data was previously reported by Bokhorst et al. (2011).