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LETTER

Cryogenic disturbance and its impact on carbon fluxes in a subarctic heathland

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Abstract

Differential frost heave, along with the associated cryogenic disturbance that accompanies it, is an almost universal feature of arctic landscapes that potentially influences the fate of the soil carbon (C) stored in arctic soils. In this study, we quantify how gross ecosystem photosynthesis (GEP), soil respiration (R_e) and the resulting net ecosystem exchange (NEE) vary in a patterned ground system (non-sorted circles) at plot-scale and whole-patterned ground scales in response to cryogenic disturbances (differential heave and soil surface disruption). We found that: (i) all studied non-sorted circles ($n = 15$) acted as net CO_2 sources (positive NEE); (ii) GEP showed a weaker decrease than R_e in response to increased cryogenic disturbance/decreased humus cover, indicating that undisturbed humus-covered sites are currently the main source of atmospheric CO_2 in the studied system. Interestingly, R_e fluxes normalized to C pools indicated that C is currently respired more rapidly at sites exposed to cryogenic disturbances; hence, higher NEE fluxes at less disturbed sites are likely an effect of a more slowly degrading but larger total pool that was built up in the past. Our results highlight the complex effects of cryogenic processes on the C cycle at various time scales.

1. Introduction

A unique feature of high-latitude soils is their large soil carbon (C) storage build-up during exposure to severe physical frost events (Ping *et al* 2008b). In these soils, the fate of C is influenced by cryogenic processes that generate differential soil heave, which varies at metre to sub-metre spatial scales owing to heterogeneities in insulation and soil moisture during the winter. Differential heave (DH) may negatively affect the fixation of C because the physical motion of frozen soil disrupts plant roots and the generated microtopography can cause increased environmental stress on plants (Jonasson 1986, Kade and Walker 2008). Further, the gravity gradient created by DH is a key driver of cryoturbation (Peterson *et al* 2003)—i.e., the lateral and vertical displacement of soil that may bury surface organic matter and reset humus formation. Cryoturbation is believed to control the long-term trajectories of soil C and subsequently also the conditions for heterotrophic microorganisms (Bockheim 2007, Koven *et al* 2009, Koven *et al* 2011). Nevertheless, the net effect on C fluxes from a combination of cryoturbation and cryogenic disturbances remains largely unquantified.

Currently, there seems to be a general consensus that the vertical translocation of C induced by cryoturbation increases the ability of the soil to accumulate C over millennial time-scales (Michaelson *et al* 1996, Bockheim 2007, Bockheim and Hinkel 2007, Koven *et al* 2009, Hugelius *et al* 2011, Koven *et al* 2011). The rationale for this assumption is that the vertical transport of C from the surface down to cold and anoxic deeper soil layers deteriorates microbial environmental conditions, controlling the heterotrophic respiration of organic matter. Soils showing morphological evidence of past vertical soil mass fluxes induced by cryoturbation also seem to contain more C than soil unaffected by this process (Ping *et al* 2008a). However, whether the subduction of C as a result of differential frost heave has a net positive effect on the C accumulation in arctic soils is not certain. Although there is a rationale for a long-term negative effect on heterotrophic respiration rates as organic rich soil layers are translocated downwards, DH, which drives the subduction, also has a short-term negative impact on plant growth (Jonasson 1986); hence, the input of C to the soil is expected to be reduced in response to cryogenic activities. In addition, soil subjected to cryogenic disturbance and uplifting by DH are often warmer in the summer than surrounding areas (Kade *et al* 2006), which could stimulate respiration losses. Even though gross ecosystem production and soil respiration rates (R_e) has been quantified in systems experiencing both subduction of soil layers and cryogenic disturbances (Wilson and Humphreys 2010), the relative importance of each of these processes for C fluxes has so far not been fully understood.

Indeed, the contrasting effects of cryogenic processes on C fluxes in combination with that these effects are expressed over different time-scales (years to millennia) makes it difficult to predict net changes in C fluxes in response to changing cryogenic conditions. However, resolving the role of cryogenic processes on the arctic soil C fluxes at different temporal scales is highly urgent, especially because the intensity of cryogenic processes is expected to decrease in many areas in the near future as a result of ongoing climate warming (Solomon *et al* 2007, Aalto *et al* 2014). In this study, we measure how gross ecosystem photosynthesis (GEP), R_e and the residual net ecosystem exchange (NEE) respond to different intensities of cryogenic disturbances. DH and soil surface disturbances were used as proxies as suggested in previous research (Klaus *et al* 2013). These estimates are important for understanding the early effects of a reduction in cryogenic disturbance on the C balance in arctic soils. In our study, we utilize a patterned ground feature referred to as non-sorted circles (also called frost boils) as a study system, in which DH and the subduction of organic soil horizons and plant growth disturbance have been documented to simultaneously occur (Walker *et al* 2004, Kade and Walker 2008, Becher *et al* 2013, Klaus *et al* 2013). The studied non-sorted circle system offered a gradient in DH that covered the range typically seen within the subarctic and high-artic regions without large differences in soil texture. The main objective of this study was to investigate the effect of cryogenic disturbance on the C cycle in cryogenically disturbed soil. We tested the following hypotheses: (i) cryogenic disturbances reduce GEP and R_e; and (ii) NEE is affected by cryogenic disturbance as a result of disproportional effects on R_e and GEP.

2. Materials and methods

2.1. Site description

Ecosystem C fluxes were measured in a patterned ground feature called non-sorted circles close to Abisko Scientific Research Station in northern Sweden (68°2′N, 18°50′E) during the year 2012 (May–October). The studied non-sorted circles were characterized by sparsely vegetated, often circular areas surrounded by a more densely vegetated rim (henceforth referred to as *outer*). The cryogenic processes within non-sorted circles have been well documented in previous studies (Kade and Walker 2008, Klaus *et al* 2013). In the centre of the non-sorted circle (henceforth referred to as *inner*), the sparsely growing plant community offers little insulation during winter, and extensive soil frost and growth of ice lenses causes the soil to heave more than the better-insulated vegetated outer. Gravity gradients generated because of this DH drive soil motion from *inner* towards *outer*, where the soil is subducted as cavities generated by thawing ice lenses underlying *inner* are filled with returning soil from *outer*, creating a pseudo-circular motion. The non-sorted circles used for the study were found in three separate fields. For each field, five non-sorted circles were investigated ($n = 15$). The area between the non-sorted circles—*outer* at the study sites was covered by a 13.2 ± 6.6 cm thick (mean ± SD) organic horizon developed under low heath vegetation such as *Empetrum nigrum*, *Vaccinium uliginosum* and *Betula nana*. In *inner*, the dominating plants were *Juncus triglumis*, *Juncus biglumis*, and *Pinguicula* sp with an organic horizon of 0.5 ± 0.4 cm. The areas between *inner* and *outer* (here referred to as *transition*) had an organic horizon of 2.1 ± 1.4 cm and were dominated by *Rhododendron lapponicum* and *Arctostaphylos alpinus*.

Long-term climatic monitoring near the study sites at the Abisko Scientific Research Station indicated that the mean annual temperature in the area during the study year (2012) was –0.86 °C, which is slightly lower than the average during the previous 100 years (–0.48 °C) and much lower than the average during the previous ten years (0.52 °C). Precipitation during the same year was 367 mm, which was slightly higher than the mean annual precipitation between the years 1913–2013 (322 mm) and during the previous ten years (302 mm). Both climatic data and monitoring of permafrost indicate that the cryogenic activity in the area is changing as the active layer has increased in mires near the study sites (Johansson *et al* 2011). Within the non-sorted circles of the Abisko area, Becher *et al* (2013) have shown using paleoecolgical studies, a long-term reduction in cryogenic activity since the beginning of the 20th century.

2.2. Measurements of environmental data

For each non-sorted circle, soil temperature and moisture were measured, with three replicates, using a portable measuring device (ML3—ThetaProbe soil moisture sensor connected to a HH2 moisture metre (Delta-T devices Ltd)) at the three plot-scales (*inner*, *transition*, and *outer*). Photosynthetic active radiation (PAR) was measured onsite using a portable PAR sensor (JYP 1000; SDEC, Reignac-sur-Indre, France). Air temperature was measured using three-hour average values (between 11 am and 12 am) at the Abisko Research Station (located between 300 and 900 m from the study sites). The height difference between *inner* and *outer* was measured in August 2012 and 2013 as well as March 2013 and 2014 using a GPS device (Trimble R7 GNSS, Trimble Navigation Limited 935 Stewart Drive Sunnyvale, California 94 085 USA) with a real-time kinematic survey technique. DH was calculated as follows:

$$Df = \left(h_{w,i} - h_{s,i}\right) - \left(h_{w,o} - h_{s,o}\right), \quad (1)$$

where h indicates the height (cm) of *inner* (i) and *outer* (o) during winter (w) and summer (s). The rationale for this was that this measurement has been shown to drive both the lateral displacements of soil (Klaus *et al* 2013) and the disturbance of plant roots (Jonasson 1986, Walker *et al* 2004, Kade and Walker 2008).

To compare the differences in cryogenic disturbances between study sites, we used a proxy for cryogenically disturbed soil; by using a 50 × 50 cm frame with 25 squares (10 × 10 cm), the number of squares (N) with more than 1 cm^2 of disrupted mineral soil surface lacking vegetation or humus (S) was counted, and the cryogenic activity index ($Cryo_{index}$) was calculated:

$$Cryo_{index} = \frac{S}{N}. \quad (2)$$

As a measure of the photosynthetic activity, we calculated the normalized difference vegetation index (NDVI) at all plot-scales (*inner*, *transition*, and *outer*) for all 15 non-sorted circles during the peak growing season (days of the year 228 and 232 during 2012 and days of year 230–231 during 2013) using an NDVI-programmed Canon EOS Digital Rebel XSi camera with an Canon Ultrasonic 20–35 mm lens. Each picture was captured from a height of approximately 1 m directly above a 50 × 50 cm frame and processed with WinCAM 2012a (Regent instruments Inc.) by calculating the average NDVI value within the 50 × 50 cm frame.

2.3. Soil excavation and analysis

Soil cores, taken with a steel auger with a diameter of 2 cm, were used to extract the soil from *inner*, *transition* and *outer*. Soil horizons were identified using colour and texture and sub-sectioned in the field. Identification of soil horizons was facilitated by clear differences in colour between the O horizon and the underlying mineral soil layers (A, C and buried O horizons). When the horizon layer was larger than 10 cm, it was divided into 10 cm pieces, placed in plastic bags and stored in a freezer before further analysis. The samples were freeze-dried, and 8.5–10.9 mg of mineral soil and 2.6–4.2 mg of organic material were transferred to silver capsules and treated with HCl to remove carbonates, using a modification of the original method by Hedges and Stern (1984). Soil organic C concentrations were measured using a Perkin-Elmer 2400 Series II CHNS/O-analyser (operating in CHN mode). C storage for each horizon and site was calculated from the C%, density and amount of soil <2 mm down to a depth of 50 cm, where C% in the lowest sampled horizon was used extrapolate down to that depth.

2.4. CO_2 flux measurements and calculations

Carbon dioxide (CO_2) flux measurements were taken by infrared gas analysis at three plot-scales within each non-sorted circle (*inner*, *transition* and *outer*) every second week during the summer 2012 ($n = 537$). We used a closed system with a CPY-2 canopy exchange chamber (PP Systems), 145 mm height × 164 mm diameter, attached to an EGM-4 infrared gas analyser (PP Systems). The chamber was sealed to the ground by attaching it to clear Perspex collars (147 mm in diameter and 90 mm high) with a connected clear vinyl skirt, which was sealed to the ground surface with a heavy tube depressing the attached skirt. The chamber was placed on the same plot-scales used for vegetation mapping and measurements of DH. Measurements were taken over a period of 2 min The chamber was re-equilibrated to ambient atmospheric conditions between measurements. At each plot, we conducted flux measurements in the following order: a first measurement with an uncovered chamber—enabling photosynthesis and soil respiration to occur simultaneously (i.e., NEE) after covering the chamber to exclude all light for 2 min to enable photosynthetic activity to cease; and a second measurement in dark conditions (i.e., R_e). NEE and R_e fluxes were used to calculate the gross ecosystem photosynthesis (i.e., GEP):

$$\mathrm{GEP} = \mathrm{NEE} - R_e, \quad (3)$$

where negative NEE values indicate the sink of CO_2 into the atmosphere.

2.5. Statistical analysis

Linear models were used to evaluate the relationship between (i) NDVI and GEP in 2012 and (ii) NDVI and NEE in 2012. A correlation test was performed for (i) NDVI in 2012 and NDVI in 2013 and (ii) DH in 2012 and DH in 2013. The variables were not normal distributed, and a Spearman's correlation coefficient was used. An ANOVA was performed to analyse whether the two plot-scales, *inner* and *outer*, had a significant effect on heave (IC_w-IC_s and C_w-C_s, parameters from equation (1)). Further, a one-way ANOVA was used to analyse the effect of (i) cryogenic activity index, (ii) soil temperature, (iii) moisture, (iv) total C storage, (v) C storage in mineral soil, (vi) O horizon, and (vii) R_e expressed per C stored in the three plot-scales (*inner*, *transition* and *outer*). Total C storage, C storage in mineral soil, O horizon and R_e

expressed per C stored did not meet the assumption of heteroscedasticity and were therefore logarithmically transposed to improve the model. A one-way ANOVA was also used to analyse whether the C storage at a plot-scale was different between locations. All one-way ANOVAs were followed by a post-hoc Tukey test to separate the groups if a statistically significant result was found. To analyse the effect of cryogenic disturbance, linear regression models were created for each C flux and NDVI, with the cryogenic activity index as the explanatory variable and NEE, R_e, GEP and NDVI as the response variables. NEE, R_e, GEP and NDVI did not meet the assumption of heteroscedasticity and were therefore logarithmically transposed to improve the model. A linear regression was performed with a summarization of R_e expressed per SOC stored for each non-sorted circle (*inner*, *transition* and *outer* were added together). All statistical analysis was performed in R 3.0.2 (R Core Team 2014).

3. Results

The studied non-sorted circle system showed a large variation during the summer season in terms of soil temperature and moisture, which ranged between – 1 °C and 18 °C and 1% and 75%, respectively (figure 1, table S1). Average soil temperature increased during the summer and reached its maximum in mid-August (day of the year 227) (figure 1). Air temperature showed a higher variation, but followed a similar temporal trend. Soil moisture was highest in the early summer (day of the year 136) and decreased during the summer. Soil temperature was significantly higher in *inner* than in *transition* and *outer* ($F_{2,42} = 77.81$, $p < 0.001$; figure 2), but no significant differences in the seasonal soil moisture (mean values) were noted (table S1).

The studied cryogenic disturbance proxies varied greatly both within and between non-sorted circles, where DH of individual non-sorted circles ranged from 2 to 22 cm (table S1) and the cryogenic activity index ranged between 0 and 1. The DH measured for individual non-sorted circles during the years 2012 and 2013 was highly correlated (rho = 0.96), suggesting a repeated pattern of ice-lens formation and cryogenic disturbance at the sites. Heave was higher in *inner* ($F_{1,28} = 12.7$, $p = 0.001$) than in *outer*, and values for the cryogenic activity index ($Cryo_{index}$, equation (2)) showed a similar pattern in which values were significantly lower in *transition* and *outer* than in *inner* ($F_{2,42} = 14.63, p < 0.001$).

GEP and R_e varied during the season with no clear temporal trend (figure S1), and the season average was used for further analyses (table S1). Furthermore, the variation of NDVI between years 2012 and 2013 was strongly correlated (rho = 0.82), suggesting that trends in photosynthetic activity are repeated between years.

In line with our hypothesis, GEP and R_e decreased with increasing cryogenic disturbance measured, using the cryogenic activity index as a proxy ($p < 0.001$, $r^2 = 0.46$, and $p < 0.001$, $r^2 = 0.43$, respectively; figures 3(a) and (b)). NDVI was significantly related to GEP ($p < 0.001$, $r^2 = 0.6$; figure 4(a)) and cryogenic disturbance ($p < 0.001$, $r^2 = 0.27$), validating the measured GEP estimates. Further, the combined effect of GEP and R_e result in a decreased NEE with increasing cryogenic disturbance (and decreased humus cover) indicated by the cryogenic activity index ($p = 0.0227$, $r^2 = 0.09$, figure 3(c)). NEE was positively related to NDVI ($p < 0.001, r^2 = 0.29$; figure 4(b)).

Carbon pools varied significantly within the studied circles at a plot-scale scale—i.e., between *inner*, *transition* and *outer* ($F_{2,42} = 60.68$, $p < 0.001$; figure 5(a)). Here, O-horizon C storage in *inner* and *transition* was statistically significantly lower than in *outer* ($F_{2,42} = 185.19$, $p < 0.001$; figure 5(a)). R_e fluxes normalized to the underlying C pool were higher in *inner* and *transition* than in *outer* ($F_{2,42} = 15.95, p > 0.001$; figure 5(b)). Further, when summarizing R_e fluxes at the whole-patterned ground scale, there was a positive relationship between DH and R_e fluxes normalized to the total C pool ($p = 0.04$, $r^2 = 0.21$; figure 5(c)).

4. Discussion

We studied an area characterized by a strong gradient in DH and soil surface disturbance due to cryogenic processes. Our gradient represents an approximate anology for the DH variability seen along the larger-scale North American bioclimatic gradient studied previously by Walker *et al* (2004). DH increases the instability of the soil surface and co-varies with soil surface disturbance and the subduction of organic soil layers (Kade and Walker 2008, Klaus *et al* 2013). In the studied gradient, the highest DH measurements represent values directly comparable to the most cryogenically active non-sorted circle sites in the study area (Klaus *et al* 2013) and in North America (Michaelson *et al* 2008), whereas some of the weakly heaving non-sorted circles are comparable to inactive sites. In other words, the range of cryogenic disturbance and vertical soil subduction induced by DH in the studied gradient is expected to represent a large portion of the arctic.

In line with our first hypothesis, GEP was negatively related to cryogenic activity. The negative correlation between NDVI and the cryogenic activity index indicates that the reduced photosynthetic activity is caused by reduced plant abundance because disturbances by cryogenic processes increase. Cryogenic processes can influence GEP through two separate mechanisms. First, DH disrupts roots and thus decreases plant production (Jonasson 1986). Second,

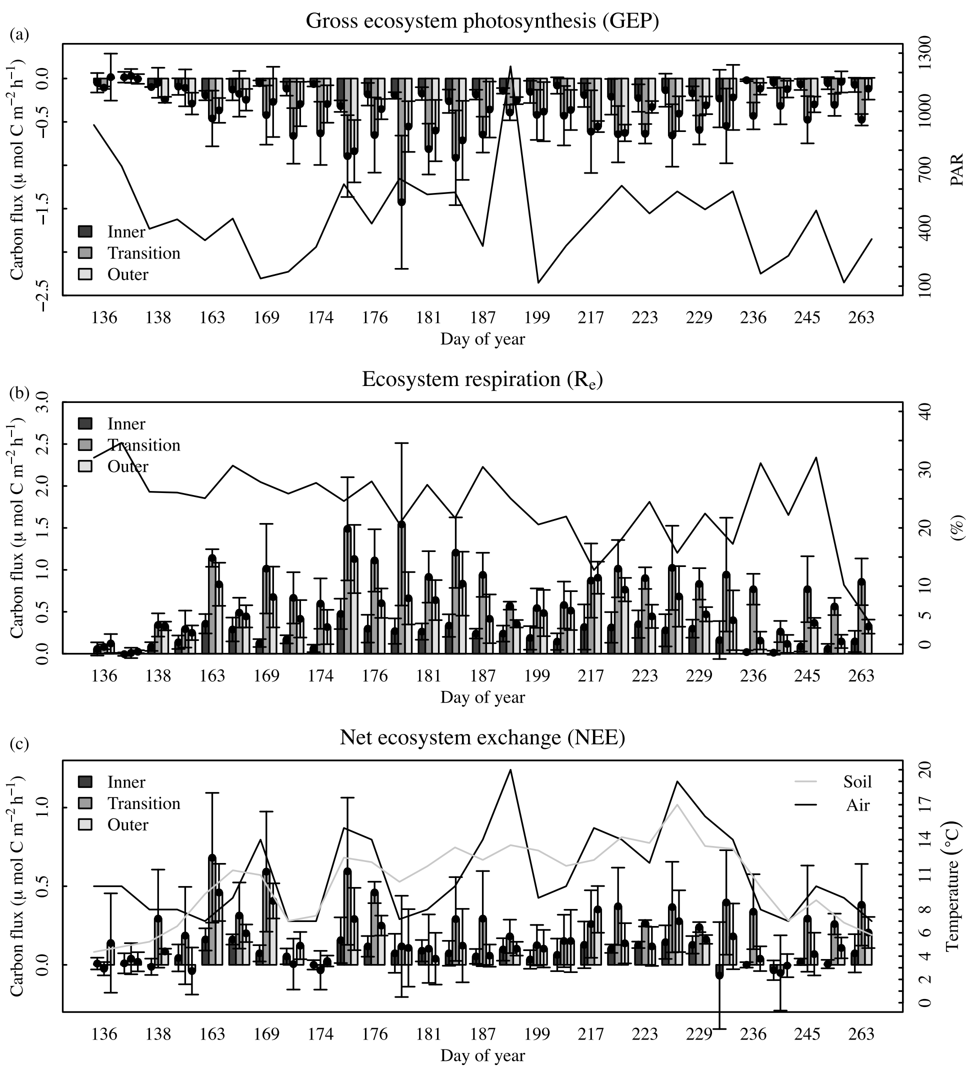

Figure 1. C fluxes and environmental data during the growing season. Daily average of all non-sorted circles measured for GEP (a), R_e (b) and NEE (c) for *inner*, *transition*, and *outer* over the growing season. Measured values for PAR (a) soil moisture (b) and air temperature are shown in solid lines, whereas soil temperature is shown as a dashed line (c). Note that all of the latter variables are plotted using the right *y*-axis.

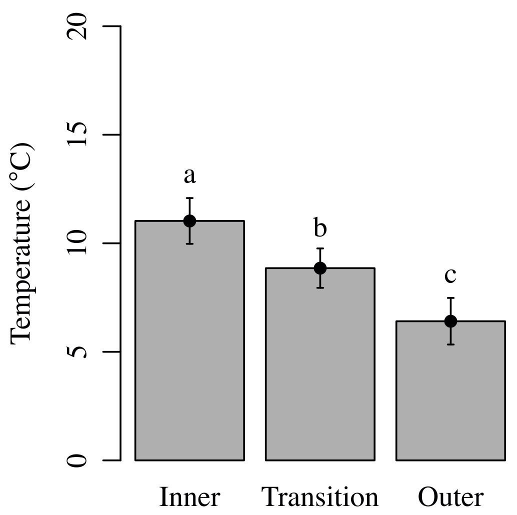

Figure 2. Effect of temperature in the three plot-scales (*inner*, *transition*, and *outer*). Error bars indicate standard deviation. Groups not sharing letters indicate statistically significant differences ($p < 0.05$).

ice lenses formed in the heaving soil and on the soil surface can cause damage to belowground and aboveground plant components. Measured GEP values for the plot-scales least affected by cryogenic disturbances (*outer*) are comparable to previously published GEP values for *outer*. For example, Kade *et al* (2012) estimated a growing season average of approximately –0.5 μmol C m^{-2} s^{-1} for *outer* in arctic Alaska, which is close to the seasonal mean of –0.5 ± 0.2 μmol C m^{-2} s^{-1} ($n = 15$). Nevertheless, the GEP at the *outer* site may still be hampered by cryogenic processes similar to such areas in which non-sorted circles are affected by cryogenic activities in the mineral soil (Harris 1998). Such disturbance could explain why a stable soil developing in an *Empetrum*-dominated tundra site close to our study site has much higher GEP—i.e., approximately –1.2 μmol C m^{-2} s^{-1} (Cahoon *et al* 2012). Considering the fact that the GEP more than doubled at this site despite comparable vegetation communities, it seems likely that our

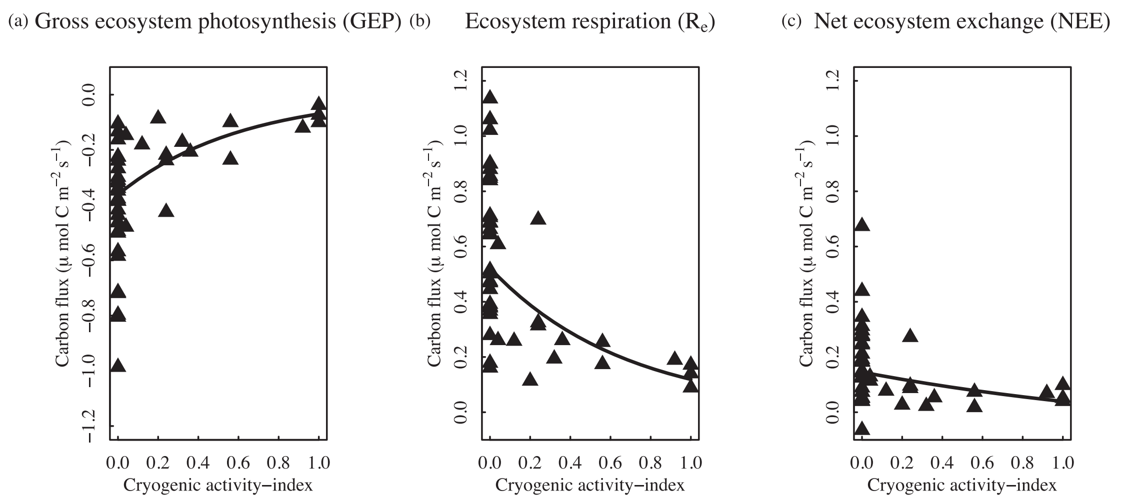

Figure 3. Relationship between cryogenic activities and C fluxes for all plot-scales within the studied non-sorted circles: (a) gross ecosystem photosynthesis (GEP) as a function of the cryogenic activity index ($p < 0.001, r^2 = 0.46, y = -1.65x^{-1.02}$); (b) soil respiration rate (R_e) as a function of the cryogenic activity index ($p < 0.001, r^2 = 0.43, y = -1.48x^{-0.65}$) and; (c) net ecosystem exchange (NEE) as a function of the cryogenic activity index ($p = 0.027, r^2 = 0.09, y = -0.57x^{-1.4}$).

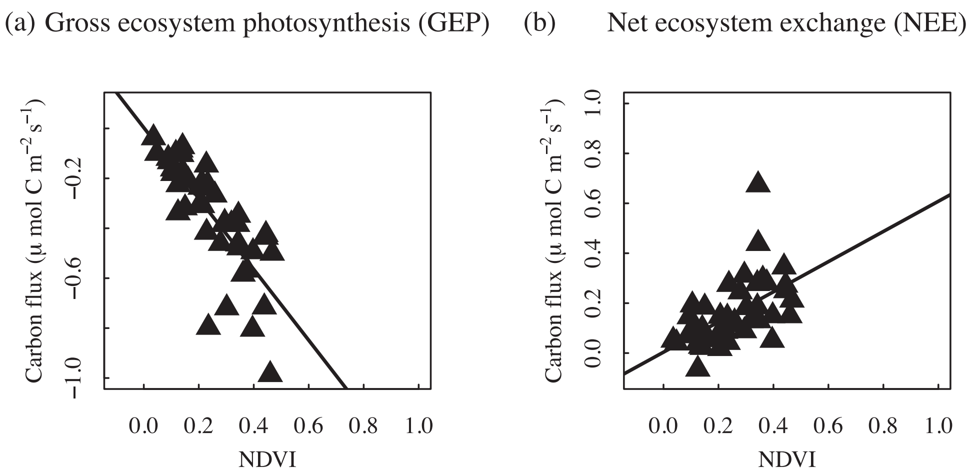

Figure 4. Relationship between the normalized difference vegetation index (NDVI) and C fluxes in the studied non-sorted circles. A solid line indicates a statistically significant relationship for (a) gross ecosystem production (GEP) ($p < 0.001, r^2 = 0.6$, $y = 0.00 - 1.42x$) and (b) net ecosystem exchange (NEE) ($p < 0.001, r^2 = 0.29, y = 0.00 + 0.60x$). NDVI-values are from days 228 and 232 in the year 2012, and growing season averages of GEP and NEE are reported.

studied gradient does not include sites completely undisturbed by cryogenic processes. However, 2012 featured a cold summer, which also could have contributed to the low GEP values in this study.

Cryogenic processes not only negatively affected the plant input of C to the ecosystem but also decreased the respiration rate. Ecosystem respiration rates result from the combined efflux of CO_2 from plant respiration and heterotrophic respiration of soil C. It is therefore not surprising to find that soil respiration decreases in a similar manner to GEP with increasing cryogenic activities, as GEP affects both the build-up of soil C and root respiration. The normalized R_e flux, taking into account the variable C pools, reveals that the reason why R_e decreases faster than GEP is unlikely to be a result of decreased heterotrophic respiration rates in *inner* because the normalized respiration rates indicate the opposite; in fact, respirations rates are faster in *inner* and *transition* than in *outer*. This higher respiration rate cannot be explained by a higher root respiration loss because GEP is much lower in *inner* and *transition*. The faster respiration rates in the latter two plots-scales are more likely to be induced by the higher average soil temperatures at these two sites. However, a positive effect of more intense surface mixing by cryogenic processes could also contribute since short-term heterotrophic respiration is stimulated by mixing these two materials (Klaminder *et al* 2013). Interestingly, higher normalized respiration rates in response to increased cryogenic disturbance is seen not only at a plot-scale scale but also for each non-sorted circle, in which increased DH appears to generate increased respiration rates.

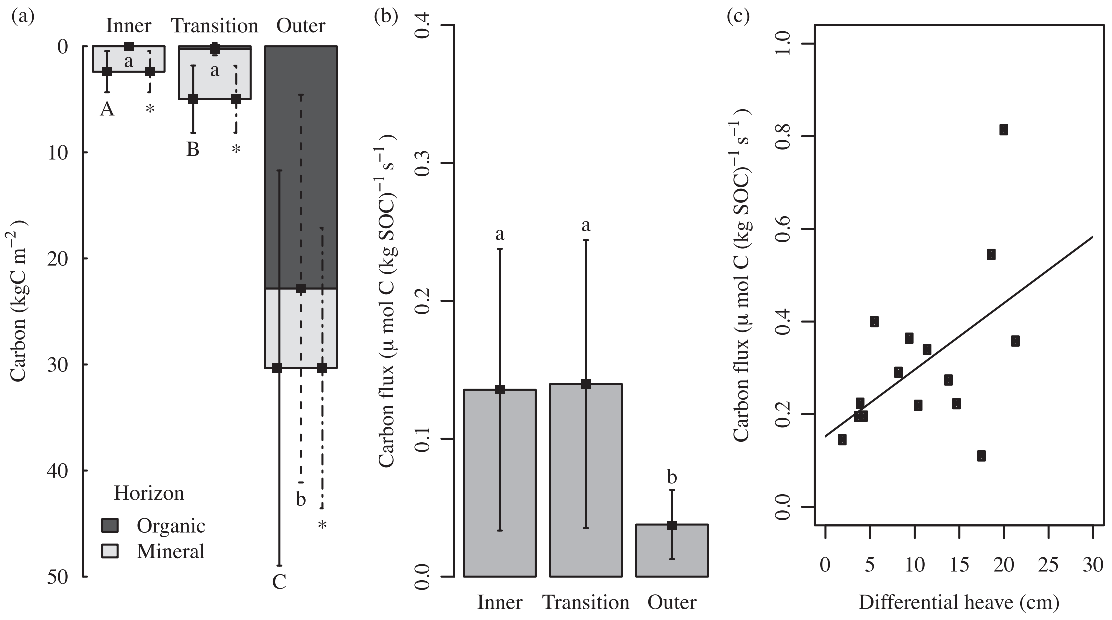

Figure 5. (a) Carbon storage in mineral soil and O horizon of the studied plot-scales (*inner*, *transition*, and *outer*), where pools in the organic and mineral horizon are represented as dark and light grey, respectively; (b) ecosystem respiration (R_e) normalized for the total carbon storage (mineral soil + O horizon) for the same three plot-scales; and (c) ecosystem respiration (R_e) normalized for the total carbon storage (mineral soil + O horizon) for each patterned ground unit (non-sorted circle) as a function of differential frost heave (cm) for each circle ($p = 0.04$, $r^2 = 0.21$, $y = 0.15 + 0.01x$). Error bars indicate standard deviation in all panels (in panel (a) solid error bars corresponds to total carbon storage, dashed error bars to carbon storage in O horizon and dot-dash error bars corresponds to carbon storage in mineral soil). Groups not sharing letters indicate statistically significant differences ($p < 0.05$).

Why are sites with organic matter that respires at a higher rate a weaker source of CO_2, a finding that at a first glance appears counterintuitive? This finding can be explained by the larger C pool accumulated in the O horizon of the *outer* zone; even though the respiration rate is slower, the cumulative soil respiration flux released from this area is higher than that from the small C pool turning over in the *inner* zone. The age of this respired C cannot be determined by our approach. Previous studies have found that respiration losses in cryoturbated soils originates from a mixture of both old and recently fixed C where the latter are often the dominant source (Wookey *et al* 2002, Czimczik and Welker 2010). The Abisko area has experienced a warmer climate during the last decades (Callaghan *et al* 2010). We attribute the apparent stronger release of C from the thicker humus packs in the *outer* zone as an indication that organic matter, accumulated as humus during colder conditions in the past, is currently serving as a respiration source in response to the recent warming. If true, this suggest that, accumulated in the form of humus that is not exposed to cryogenic burial processes, can release its C pool without a proportional increase in GEP during periods of changing climatic conditions.

5. Conclusions

Our findings indicate a complex influence of cryogenic activities on C fluxes in the studied systems, occurring over small spatial gradients as well as in different time periods. Currently, cryogenic activities are, in a time scale of years, associated with a lower NEE and thus a higher potential for C accumulation. If cryogenic disturbance processes co-occur with the burial and prevention of a build-up of C in the form of humus at the mineral soil surface, the effect of cryogenic disturbances is expected to generate a lower NEE at a centennial to millennial time scale, as suggested by others (Bockheim 2007, Koven *et al* 2009). However, it is also clear that cryogenic disturbance has the capacity to lower GEP and thus lower the input of C to the soil at an annual time scale. The outlined complexity is further enhanced because the mineralization rate of organic matter can be accelerated by cryogenically driven processes—either indirectly as soil temperature during summer increases in response to reduced humus cover or directly by the mixing of surface soil, which appears to stimulate heterotrophic respiration. The highlighted complexity is further indicated by the positive relationship between NEE and NDVI found in this study, which stands in complete contrast to the commonly assumed negative relationship used to predict CO_2 fluxes in arctic landscapes (Shaver *et al* 2007, Dagg and Lafleur 2014). Contrasting trends have important implications for how NDVI can be used for upscaling C fluxes in the arctic from satellite data, which suggests that relationships between NEE and NDVI established for sites less affected by cryogenic processes have limited predictive power in soils under the influence of cryogenic disturbance processes. Finally, cryogenic activities are predicted to decrease in large parts of the northern hemisphere (Aalto *et al* 2014). It is evident from our study that these changes will affect important C fluxes and that changing conditions for cryogenic activities needs to be considered when predicting the fate of C in high latitude ecosystems.

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