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1 **Seasonally different response of photosynthetic activity to daytime and night-time**  
2 **warming in the Northern Hemisphere**

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19

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## 1 **Abstract**

2 Over the last century the Northern Hemisphere has experienced rapid climate warming, but  
3 this warming has not been evenly distributed seasonally, as well as diurnally. The implications  
4 of such seasonal and diurnal heterogeneous warming on regional and global vegetation  
5 photosynthetic activity, however, are still poorly understood. Here, we investigated for  
6 different seasons how photosynthetic activity of vegetation correlates with changes in  
7 seasonal daytime and night-time temperature across the Northern Hemisphere ( $>30^{\circ}\text{N}$ ), using  
8 Normalized Difference Vegetation Index (NDVI) data from 1982 to 2011 obtained from the  
9 Advanced Very High Resolution Radiometer (AVHRR). Our analysis revealed some striking  
10 seasonal differences in the response of NDVI to changes in day- versus night-time  
11 temperatures. For instance, while higher daytime temperature ( $T_{\text{max}}$ ) is generally associated  
12 with higher NDVI values across the boreal zone, the area exhibiting a statistically significant  
13 positive correlation between  $T_{\text{max}}$  and NDVI is much larger in spring (41% of area in boreal  
14 zone – total area  $12.6 \times 10^6 \text{ km}^2$ ) than in summer and autumn (14% and 9%, respectively). In  
15 contrast to the predominantly positive response of boreal ecosystems to changes in  $T_{\text{max}}$ ,  
16 increases in  $T_{\text{max}}$  tended to negatively influence vegetation growth in temperate dry regions,  
17 particularly during summer. Changes in night-time temperature ( $T_{\text{min}}$ ) correlated negatively  
18 with autumnal NDVI in most of the Northern Hemisphere, but had a positive effect on spring  
19 and summer NDVI in most temperate regions (e.g., Central North America and Central Asia).  
20 Such divergent covariance between the photosynthetic activity of Northern Hemispheric  
21 vegetation and day- and night-time temperature changes among different seasons and climate  
22 zones suggests a changing dominance of ecophysiological processes across time and space.

1 Understanding the seasonally different responses of vegetation photosynthetic activity to  
2 diurnal temperature changes, which have not been captured by current land surface models, is  
3 important for improving the performance of next generation regional and global coupled  
4 vegetation-climate models.

5

6

7

## 1 **1. Introduction**

2 Vegetation is an important component of the Earth system, playing an important role in  
3 modulating regional and global climate change through biogeochemical and biophysical  
4 feedbacks (Field et al., 2007; Peñuelas et al., 2009). Biological characteristics of vegetation,  
5 such as photosynthetic capacity, length of the growing season, and plant population dynamics  
6 are usually sensitive to climate change (Myneni et al., 1997; Root et al., 2003; Adams et al.,  
7 2009; Peñuelas et al., 2013). Over the last decades, annual trends in NDVI and in the  
8 amplitude of the annual fluctuations in atmospheric CO<sub>2</sub> concentration (Graven et al., 2013)  
9 both indicate that global change has promoted photosynthetic activity and growth of  
10 vegetation across the Northern Hemisphere (Keeling et al., 1996; Peng et al., 2011). In  
11 temperate and boreal regions, photosynthetic activity is typically characterized by a marked  
12 seasonal cycle. Because the consecutive phenological and ontogenetic stages are dominated  
13 by different ecophysiological processes, also the climatic requirements may vary across the  
14 different phenological stages. Hence, the response of vegetation photosynthetic activity to  
15 climate variations is dependent upon season (Xu et al., 2003; Yu et al., 2003; Richardson et al.,  
16 2010). In its latest Assessment Report, the Intergovernmental Panel of Climate Change (IPCC)  
17 Assessment Report provides further evidence that climate warming is asymmetric among  
18 different seasons and continents (IPCC, 2013). For instance, the seasonality of temperature is  
19 diminishing at high latitudes because of faster warming in winter and spring than in summer  
20 (Xu et al., 2013). Similarly, night-time temperatures have been increasing faster than daytime  
21 temperatures globally since 1950s, although this phenomenon is not temporally or spatially  
22 uniform in observation (IPCC, 2013). A better understanding about the implications of such

1 diurnal and seasonal asymmetry in global warming on regional and global vegetation  
2 photosynthetic activity will be helpful for improving our quantification of global vegetation  
3 response to climate change in the past and the future (Still, 2013).

4

5 Here we present an analysis, separately for spring, summer and autumn, of how vegetation  
6 photosynthetic activity is associated with changes in daytime and night-time temperature  
7 across the northern Hemisphere ( $>30^{\circ}\text{N}$ ) from 1982 to 2011, using time series data set of the  
8 Normalized Difference Vegetation Index (NDVI) obtained from the Advanced Very High  
9 Resolution Radiometer (AVHRR) and associated climate datasets. Although some other  
10 recent modern satellite products, such as FPAR and LAI (Myneni et al., 2002, Baret et al.,  
11 2007), may be better in measuring photosynthetic activity, these products have not been  
12 available for a sufficiently long period. The data set of the AVHRR-NDVI, by contrast, has  
13 been widely considered a useful syntheical integrator of the environmental conditions that  
14 regulate phenology and productivity (Pettorelli et al., 2005; Piao et al., 2006; Zeng et al., 2013)  
15 for three decades. Analyses of field experiments (Penueles et al., 2004; Wan et al., 2009) and  
16 satellite observations (Peng et al., 2013; Xia et al., 2014) have shown that day- and night-time  
17 warming could have different impacts on growing-season mean NDVI because the direct and  
18 indirect mechanisms by which temperature impacts on productivity differ between day and  
19 night. Given that different ecophysiological processes dominate plant activity in different  
20 phenological stages, one can also expect the response of NDVI to day- and night-time  
21 warming to vary among seasons. Thus, seasonal variation in vegetation response to global  
22 warming may add to the complexity of the phenomenon discovered by Peng et al. (2013),

1 while on the other hand it may also provide clues to better understand the geographical  
2 differences in the productivity response to daytime and night-time warming. Such information,  
3 however, has not been extensively documented in the literature. It is therefore our primary  
4 goal to understand how changes in daytime and night-time temperature during different  
5 seasons influence the vegetation photosynthetic activity of the northern temperate and boreal  
6 regions. Documenting the seasonal variation in the impacts of daytime and night-time  
7 warming on vegetation photosynthetic activity provides us a better understanding of how  
8 current and future climate change may impact on vegetation activity and thereby on the global  
9 carbon cycle, and is critical for efficient vegetation management in a rapidly changing world.  
10 A second objective of this study is to assess whether or not these satellite-based ecosystem  
11 responses to the uneven warming are captured by two global land surface models:  
12 ORCHIDEE (Krinner et al., 2005) and NCAR\_CLM4CN (Oleson et al., 2010).

13

## 14 **2. Dataset and Methods**

### 15 **2.1. Datasets**

16 We used the third generation NDVI dataset produced by the Global Inventory Monitoring and  
17 Modeling Studies (GIMMS) group for the period of January 1982 to December 2011 (Pinzon  
18 et al., 2013). These data are generated at 1/12 degree and composited over approximately 15  
19 days periods with the Maximum Value Compositing Technique (Holben et al., 1986). This  
20 data set has been calibrated for sensor changeover (satellite sensor systems have experienced  
21 many changeovers: from NOAA 7 to NOAA 9, from NOAA 9 to NOAA 11, from NOAA 11  
22 to NOAA 14, from NOAA 14 to 16, and from NOAA 16 to 18), and corrected against sensor

1 degradation, satellite orbit drift and changed solar zenith angles (Zhou et al., 2001; Tucker et  
2 al., 2005; Luo et al., 2013). Compared with previous versions of the GIMMS NDVI datasets,  
3 this version has improved in data quality, particularly in high latitudes where the growing  
4 season is shorter. To further eliminate noise and bias caused by clouds, atmospheric  
5 disturbance and changes in solar angle (Holben 1986; Tucker et al., 2005), we used monthly  
6 NDVI values, which were determined as the maximum value of the two NDVI composites of  
7 each month. This data set has recently been successfully applied for detecting changes in  
8 vegetation photosynthetic activity (Peng et al., 2011; Xu et al., 2013).

9  
10 The climate data (maximum daily temperature ( $T_{\max}$ ), minimum daily temperature ( $T_{\min}$ ),  
11 precipitation, shortwave solar radiation) used in this study covered the period 1982-2011 and  
12 had a spatial resolution of 0.5 degree. These data were monthly aggregated from the CRU TS  
13 3.20 climate dataset obtained from the Climate Research Unit (CRU), University of East  
14 Anglia (Mitchell & Jones, 2005) and the 0.5 degree CRU-NCEP data set (1901-2010), which  
15 is a combination of CRU TS.3.2 0.5 degree monthly climatology data and 2.5 degree National  
16 Centre for Environmental Prediction (NCEP2) reanalysis data from 1948 to near real time.  
17 Due to the lack of observed solar radiation data during the study period, we used cloud data  
18 (CRU) as surrogates of observed solar radiation.

19  
20 **2.2 Carbon Cycle models**

21 Two process-based land surface models simulated leaf area index (LAI) and carbon fluxes  
22 (gross primary productivity, GPP; net primary productivity, NPP) with a spatial resolution of

1 0.5 degree for the period from 1982 to 2010. These two models are ORCHIDEE (Krinner et  
2 al., 2005) and NCAR\_CLM4CN (Oleson et al., 2010; Lawrence et al., 2011), which both  
3 have been widely used to investigate regional and global land carbon fluxes (e.g. Sitch et al.,  
4 2008), as well as their responses to climate change and their feedbacks to the climate system  
5 (Thornton, et al., 2007). Models were forced with reconstructed historical climate fields and  
6 rising atmospheric CO<sub>2</sub> concentration. Both models used the same climate forcing files from  
7 the CRU-NCEP v4 dataset with 6 hourly time step  
8 (<http://dods.extra.cea.fr/data/p529viov/cruncep/>).

9

### 10 **2.3 Analyses**

11 Partial correlation analysis was used to statistically distinguish the influence of interannual  
12 changes in  $T_{\max}$  and  $T_{\min}$  on vegetation NDVI across different seasons. Partial correlation  
13 yields the correlation between two variables, while controlling for a third or more variables  
14 (Kendall 1946, Baba et al., 2004). If the partial correlation approaches 0, the inference is that  
15 any direct correlation was spurious. Since precipitation and solar radiation may also influence  
16 NDVI (Nemani et al., 2003), variations in precipitation and cloudiness were also taken into  
17 account in the partial correlation analysis. NDVI and all relevant climate variables were  
18 detrended by a linear detrending method (Peng et al., 2013) before the partial correlation  
19 analysis. We also used the LAI, GPP and NPP output of the two land surface models to verify  
20 whether these models can capture the same relationships between vegetation photosynthetic  
21 activity and  $T_{\max}$  and  $T_{\min}$ , as indicated by the remote sensing-based analyses. Note these two  
22 models are forced with climate data from the CRU-NCEP, instead of that from the CRU.

1 Accordingly,  $T_{\max}$  and  $T_{\min}$  from the CRU-NCEP are used for the partial correlation analysis  
2 of the model simulated results.

3

4 Following Zhou et al. (2001), we defined the spring, summer, and autumn seasons as the  
5 periods from April to May, June to August, and September to October, respectively. To ensure  
6 the robustness of the estimated temperature sensitivity of seasonal NDVI to these season  
7 definitions, we repeated the analyses with modified definitions of spring, summer, and  
8 autumn; as the period from May and June, July to August, and September and October,  
9 respectively; and as the period from green-up to maturity, maturity to senescence and  
10 senescence to dormancy respectively. The transition dates for those key phenological phases  
11 have been derived by MODIS dataset (Zhang et al., 2003) and the months where multi-year  
12 averaged transition dates located are the boundaries for each season period.

13

### 14 **3. Results**

15 During spring, vegetation NDVI in the Northern Hemisphere was predominantly positively  
16 correlated with daytime temperature ( $T_{\max}$ ) change (Fig.1a). However, these responses clearly  
17 differed between latitudinal zones. In the boreal zone ( $>50^{\circ}\text{N}$ ), 89% of the land area showed a  
18 positive correlation between NDVI and  $T_{\max}$  (red lines in Fig.2a). Although this correlation  
19 was statistically significant only in about 41% of the area, significant negative correlations  
20 between NDVI and  $T_{\max}$  did not occur during spring (red lines in Fig.2a). In contrast to the  
21 boreal zone, during spring the temperate regions ( $30^{\circ}\text{N}$ - $50^{\circ}\text{N}$ ) showed a statistically  
22 significant positive correlation between NDVI and  $T_{\max}$  only in 12% of the land area (red lines

1 in Fig.2b). These significant positive spring-time correlations between NDVI and  $T_{\max}$  in the  
2 temperate zone were found mainly in the wetter or cooler regions, such as western America,  
3 southern China and the Tibetan Plateau (Fig.1a, Fig. S1). In addition, negative correlations  
4 between NDVI and  $T_{\max}$  did occur during spring in some temperate areas, mostly in arid and  
5 semi-arid regions, such as Central North America, temperate China and Central Asia (Fig.1a,  
6 Fig. S1), although only a small fraction of these were statistically significant.

7  
8 While in springtime the correlation of NDVI with  $T_{\min}$  was predominantly negative,  
9 especially in the boreal zone, night-time warming exhibited a strikingly different pattern  
10 (Fig.1b). First, vegetation NDVI correlated more frequently negatively than positively with  
11  $T_{\min}$  in the boreal regions (Fig. 1b and red lines in Fig. 2c). Many boreal areas in which NDVI  
12 correlated positively with  $T_{\max}$ , correlated negatively with  $T_{\min}$ . A similar observation can be  
13 drawn for the temperate zone: areas that tended to correlate positively with  $T_{\max}$ , correlated  
14 negatively with  $T_{\min}$  (mainly wet or cool temperate regions), and vice versa in the arid and  
15 semi-arid regions (compare Fig. 1a with Fig.1b; Fig. S1).

16  
17 During summer, NDVI was less responsive to interannual changes in  $T_{\max}$  or  $T_{\min}$  (Fig. 1c, 1d)  
18 than in spring. In boreal regions, summer NDVI remained positively correlated with  $T_{\max}$  in  
19 most areas, but the correlation was statistically significant only in 14% of the area (Fig.1c, 2a).  
20 In temperate regions, however, summertime daytime warming was negatively correlated with  
21 vegetation NDVI in a much larger area than in spring (compare Fig.1c with Fig. 1a). The  
22 negative correlation between summer NDVI and  $T_{\max}$  was found to be statistically significant

1 in 9% of the temperate zone, primarily in arid, semi-arid and cool regions, such as Central  
2 Asia, temperate China, Central America and Tibetan Plateau (Fig.1c, 2b and S1).

3  
4 Changes in  $T_{\min}$ , on the other hand, showed a roughly similar impact on NDVI during summer  
5 as compared to spring, although differences did occur (compare Fig.1d with Fig. 1b). Overall,  
6 both in the boreal and in the temperate zone, half of the area exhibited a positive correlation  
7 between NDVI and  $T_{\min}$ , and the other half showed a negative correlation between them  
8 (compare green lines in Fig. 2c and 2d). For example, negative correlations between summer  
9 NDVI and  $T_{\min}$  were found in eastern Europe, southern Siberia, Mediterranean, western  
10 America, as well as wet temperate regions, while positive correlations between them were  
11 mainly found in arid, semi-arid and cool temperate regions (Fig.1d, S1).

12  
13 During autumn, the spatial pattern of the NDVI correlations to changes in  $T_{\max}$  roughly  
14 resembled the springtime pattern in the temperate zone, while in the boreal zone it closely  
15 resembled the summertime pattern (compare Fig. 1e with Figs. 1a and 1c). Across the entire  
16 Northern Hemisphere, statistically significant positive correlations were found in only 9% of  
17 the area (Fig.2a and 2b). It should also be noted that, in autumn, significant negative  
18 correlations between  $T_{\max}$  and NDVI were very uncommon, occurring only in Central North  
19 America and Eastern Europe.

20  
21 In contrast to the observed correlations between NDVI and  $T_{\max}$ , the autumnal pattern of the  
22 correlation between NDVI and  $T_{\min}$  did exhibit more widespread negative correlations and

1 much fewer positive correlations as compared to spring or summer (Fig. 1f, Fig. 2c and 2d).  
2 Negative correlations outshadowed the positive correlations in both the temperate and boreal  
3 zones, but were especially common in Siberia (Fig. 1f).  
4  
5 Note the high inter-correlation between  $T_{\max}$  and  $T_{\min}$  makes the partial correlation results  
6 difficult to interpret, we also conducted an supplementary partial correlation analysis in which  
7 detrended  $T_{\max}$  and  $T_{\min}$  were replaced with their average ( $T_{\text{mean}}=(T_{\min}+T_{\max})/2$ ) and difference  
8 ( $\text{DTR}= T_{\max}-T_{\min}$ ) (Fig. S2). A significant partial correlation between NDVI and DTR is found  
9 for all the three seasons. For example, in boreal regions, NDVI is predominantly positively  
10 correlated with DTR in spring; while in dry temperate regions, the partial correlation between  
11 NDVI and DTR is negative in summer but positive in autumn. This significant partial  
12 correlation between NDVI and DTR again confirms the finding that vegetation growth  
13 responds differently to changes in  $T_{\max}$  and  $T_{\min}$ .  
14  
15 We next examined, in the different seasons, the correlations between model-simulated LAI  
16 and GPP and interannual changes in the corresponding temperature variables. The specific  
17 spatial and seasonal patterns of these correlations are shown in Fig. 3. Simulations with  
18 ORCHIDEE suggested that rising  $T_{\max}$  is generally associated with higher simulated GPP in  
19 the boreal zone and the Tibetan Plateau, a correlation that is particularly strong in spring and  
20 autumn, and weaker in summer. CLM4 showed a much smaller area with a positive response  
21 of GPP to daytime warming than ORCHIDEE. However, neither ORCHIDEE, nor CLM4  
22 simulated the seasonal dynamics of the impact of  $T_{\min}$  changes on GPP (significant at 95%

1 confidence level based on paired-samples t-tests) that the NDVI data exhibited. Among all the  
2 three seasons, positive correlations between GPP and  $T_{\min}$  were found in some boreal regions,  
3 mainly where GPP was also positively correlated with  $T_{\max}$ . Model simulated NPP showed  
4 similar spatial patterns in the responses to changes in  $T_{\max}$  or  $T_{\min}$  as that of GPP (Fig. S3).  
5 Model simulated LAI also responded differently to changes in  $T_{\max}$  or  $T_{\min}$  as compared with  
6 the NDVI-response and the models were not in good agreement (Fig. 4).

7

#### 8 **4. Discussion**

9 This study explored the seasonal variation in the response of vegetation photosynthetic  
10 activity to daytime and night-time temperature changes in the temperate and boreal regions of  
11 the Northern Hemisphere, an area with a globally important land carbon sink (Myneni et al.,  
12 2001; Pan et al., 2011). In line with results from an earlier study based on annual variables  
13 (Peng et al., 2013), we observed that over the last three decades higher inter-annual  $T_{\max}$  have  
14 been generally associated with higher vegetation activity, especially in the high latitude  
15 regions. The current study now shows that the strength of the relationship between  $T_{\max}$  and  
16 NDVI varies among seasons. Among the three seasons, spring shows the largest area with a  
17 significantly positive relationship between  $T_{\max}$  and NDVI (Fig. 1). In addition to increased  
18 soil nitrogen mineralization and availability (Shaw and Harte, 2001; Melillo et al., 2011; Hietz  
19 et al., 2011), a temperature-driven phenological shift towards earlier and longer growing  
20 seasons has been suggested to be one of the most important mechanisms for promoting  
21 northern vegetation photosynthetic activity (greening) under global warming (Myneni et al.,  
22 1997; Tucker et al., 2001; Piao et al., 2007). The weaker correlation between  $T_{\max}$  and NDVI

1 during autumn compared with spring could be linked to either lower soil moisture, surface  
2 soil frost in some regions, less radiation or plant senescence in the autumn season (Robock et  
3 al., 2000; Nijssen et al., 2001; Gauslaa et al., 2005; Zhang et al., 2013). It has been suggested  
4 that the temperature sensitivities of duration of the photosynthetic season in autumn and of  
5 autumn productivity are both smaller than that of their spring counterparts (Piao et al., 2008;  
6 Richardson et al., 2010; Chapman, 2013). In addition, one day lengthening of the growing  
7 season increases productivity more during spring more than during autumn, as expected from  
8 the longer days and higher radiation during spring (see e.g., Richardson et al., 2010). To  
9 investigate potential biases caused by different definitions of seasons in this analysis, we  
10 tested two other definitions of the three seasons (see Methods) and the results confirm the  
11 observed spatial patterns of the NDVI responses to  $T_{\max}$  or  $T_{\min}$ , although there is slight  
12 variability in the significant percentage about the response of vegetation to  $T_{\max}$  or  $T_{\min}$  (Figs.  
13 S4 and S5).

14  
15 We observed that positive anomalies in  $T_{\max}$  were associated with smaller gains of vegetation  
16 productivity in summer than in spring or autumn. Although it is known that the optimum  
17 temperature for photosynthesis is higher in summer than in spring or autumn (Berry and  
18 Björkman, 1980), our analysis therefore suggests that, summer maximum temperature in most  
19 areas is close to the optimal value for plant photosynthetic activity (Wan et al., 2005). An  
20 alternative explanation for the smaller NDVI response to  $T_{\max}$  in summer than that in spring  
21 or autumn is associated with the saturation of NDVI over dense vegetation, which is more  
22 likely to occur in summer (Fensholt et al., 2012). To test this hypothesis, we plotted the

1 percentages of areas with insignificant partial correlation ( $P > 0.05$ ) between NDVI and  $T_{max}$   
2 during summer along the gradient of NDVI values (Fig. S6). The result, however, does not  
3 support the idea that sparse vegetation is less saturated and therefore more sensitive to the  
4 change in  $T_{max}$  than dense vegetation (Fig. S6a). The same result is also observed when  
5 pixels with only positive or negative NDVI responses to  $T_{max}$  are singled out (Fig. S6b, c).  
6 Therefore, the observed reduction in summertime NDVI sensitivity to  $T_{max}$  is unlikely to be  
7 caused by the NDVI saturation effect of more closed vegetation.

8  
9 Our results further suggest that in contrast to most high-latitude ecosystems, increases in  $T_{max}$   
10 negatively influence vegetation photosynthetic activity in temperate dry regions, particularly  
11 during summer. This negative temperature sensitivity in temperate dry ecosystems may result  
12 from increased water stress via warming-induced soil moisture reduction (Llorens et al. 2004;  
13 Williams et al., 2012; Xu et al., 2013). This hypothesis is supported by the positive correlation  
14 ( $P < 0.05$ ) between the response of NDVI to  $T_{max}$  and the multi-year averaged topsoil water  
15 content over 1988-2007 in all the three seasons (Owe et al., 2008, Fig. S7). In addition, vapor  
16 pressure deficit (VPD) exponentially increases with rising  $T_{max}$ , which can further reduce soil  
17 moisture through increasing transpiration (Williams et al., 2012). The enhanced VPD coupled  
18 with reduced soil moisture can lower the duration of stomatal openness and increase the risk  
19 of hydraulic failure, and consequently reduce vegetation growth rate (Williams et al., 2012).  
20 On the other hand, reduced vegetation growth, in turn, can create an additional warming effect  
21 through the reduction in transpiration demand which increases radiation partitioning into  
22 sensible heat flux (Jeong et al., 2009). This positive feedback may further amplify the

1 negative NDVI sensitivity to changes in  $T_{\max}$  in a warming season. Thus the complex  
2 interaction between  $T_{\max}$ , soil moisture, plant transpiration and growth rate makes soil  
3 moisture an important driving factor in regulating vegetation photosynthetic activity over the  
4 dry temperate regions in summer (Ciais et al., 2005; Williams et al., 2012; Vicente-Serrano et  
5 al., 2013). Furthermore, there is increasing evidence from both field experiments and  
6 modeling studies that rising temperature can significantly change soil water availability in the  
7 root zone (Llorens et al., 2004; Huntington 2006; Xu et al., 2013), and thereby negatively  
8 affect vegetation photosynthetic activity (Peñuelas et al., 2004; Angert et al., 2005).

9

10 In both spring and autumn, the impact of reduced soil moisture on vegetation photosynthetic  
11 activity may be partly canceled out by positive warming-induced effects, such as extended  
12 growing seasons, or may be irrelevant because plant available water remains well above  
13 wilting point. This may explain the lack of negative correlation between  $T_{\max}$  and NDVI in  
14 spring and autumn across the temperate zone.

15

16 Compared to daytime warming, nighttime warming has been found to have a smaller negative  
17 influence on soil moisture (Xia et al., 2009; Peng et al., 2013). Therefore, the indirect effect of  
18 nighttime warming via a change in soil moisture is probably smaller than that of daytime  
19 warming. Similar to daytime warming, night-time warming may also impact on vegetation  
20 photosynthetic activity in opposite ways, through the action of different mechanisms. First,  
21 night-time warming can stimulate plant photosynthesis (Beier et al., 2008; Wan et al., 2009)  
22 through increased draw-down of leaf carbohydrates at night (Turnbull et al. 2002, 2004).

1 Second, night-time can also negatively impact plant photosynthesis through increasing  
2 autotrophic respiration (Peng et al., 2013). A field warming experiment at a temperate dry  
3 grassland site in China showed that nighttime warming stimulated plant photosynthesis by  
4 about 20% (Wan et al., 2009). This observation was supported by the analysis of Peng et al.  
5 (2013), who reported a general positive correlation between growing season  $T_{\min}$  and NDVI  
6 across the temperate dry regions. The increased metabolic use of leaf carbohydrates at night  
7 (Turnbull et al., 2002, 2004) could be mainly responsible for a compensation effect leading to  
8 enhanced vegetation photosynthetic activity in these regions (Wan et al., 2009). The results of  
9 this study, however, showed that the positive correlation between  $T_{\min}$  and NDVI is mainly  
10 evident in spring and summer (Fig. 1), implying that the dominant ecophysiological effects of  
11 nighttime warming vary seasonally. In most of central and western Asia, for example, a  
12 significantly positive correlation between  $T_{\min}$  and NDVI was observed during spring and  
13 summer, but autumn NDVI show significant negative correlation with autumn  $T_{\min}$ .

14  
15 Similar to the temperate zone, the direction and the strength of the  $T_{\min}$ -NDVI relationship in  
16 high latitudes shows strong seasonal variability. Opposite to the common speculation in the  
17 literature that global warming could enhance vegetation photosynthetic activity in the  
18 Northern Hemisphere (Keeling et al., 1996; Myneni et al., 1997; Zhou et al., 2001; Peng et al.,  
19 2011), the study of Peng et al. (2013) pointed out that rising  $T_{\min}$  was associated with reduced  
20 vegetation productivity in cold and wet regions. Here, we found that in the high latitude cold  
21 regions, a negative correlation between  $T_{\min}$  and NDVI is more common during autumn than  
22 during spring and summer, indicating that autumn is the main contributing season to the

1 negative response of growing season averaged NDVI to increases in growing season averaged  
2  $T_{\min}$ , as reported by Peng et al. (2013). The colder and longer nights in autumn may be part of  
3 the explanation, but further studies are needed to explore the underlying mechanisms.

4  
5 Prior research indicated that increase in maximum temperature could enhance rice yields in  
6 tropical and subtropical Asia (Welch et al., 2010). Here we also observed a positive effect of  
7  $T_{\max}$  on spring NDVI in some regions dominated by crops, such as central North American.  
8 However, a negative effect of  $T_{\max}$  on summer and autumn NDVI is also observed in those  
9 areas, likely due to heat induced chloroplast damage, spikelet sterility, higher respiration  
10 demand and greater evaporative loss (Wassmann et al., 2009, Dhakwa & Cambell 1998). The  
11 effect of  $T_{\min}$  on cropland NDVI is also very complicated. On one side, increased  $T_{\min}$  could  
12 reduce crop growth through increasing respiration losses, reducing grain-filling duration and  
13 endosperm cell size (Welch et al., 2010). On the other side, increased  $T_{\min}$  could benefit crop  
14 growth through reducing the occurrence frequency of frost events (Lobell DB et al., 2007).  
15 Thus the apparent response of crop growth to  $T_{\min}$  is the balanced result of those two opposite  
16 impacts. Additionally, it should be noted that cropland NDVI is also regulated by agricultural  
17 management, like reaping and irrigating.

18  
19 Land surface models are used to project future states of ecosystems and climate. We show  
20 here that current land surface models cannot capture the seasonal variation in the response of  
21 photosynthetic activity to daytime and night-time temperature changes across the Northern  
22 Hemisphere. This may provide some new insights on understanding the uncertainties in

1 current IPCC AR5 model projections of future changes in global carbon cycle and its  
2 feedback to climate (IPCC, 2013). It is not clear, however, if this inconsistency between  
3 satellite data analysis and modeled GPP analysis is induced by bias of climate forcing from  
4 CRU-NCEP (with 6 hour temporal resolution) or in modeled vegetation productivity due to  
5 the inaccurate representation of physical process (such as soil moisture) or the missing  
6 ecophysiological process (e.g., the response of plant photosynthesis to nighttime warming  
7 through altered draw-down of leaf carbohydrates at night) in the models. In addition to the  
8 direct impacts on plant photosynthesis and respiration, warming could also profoundly alter  
9 plant community structure and composition (Wu et al., 2012; Peñuelas et al., 2013), which  
10 has also important implications for ecosystem productivity (Wang et al., 2012; Liu et al.,  
11 2013). Such warming-induced changes in plant community structure and composition may  
12 play a more important role in regulating the response of vegetation productivity to  
13 temperature change in grasslands than in forests. One can expect that the structurally changed  
14 plant community may bring further changes in the seasonal variability of the vegetation  
15 photosynthetic activity response to temperature change, given the differences in phenology  
16 among different vegetation types.

17

18 In summary, we here show differences in vegetation activity correlations to diurnal  
19 temperature changes across different seasons and regions in the Northern Hemisphere. Our  
20 results suggest that the diurnal and seasonal variations in vegetation responses to temperature  
21 changes are important for understanding the changes in vegetation photosynthetic activity in a  
22 warming world. Such diurnal and seasonal variations, however, have rarely been incorporated

1 in current experimental and modelling studies on vegetation responses to global warming  
2 which are overwhelmingly based on daily or growing season mean air temperature. New field  
3 warming experiments with differently elevated temperature during day versus night, and  
4 across different seasons, are urgently needed. Such experiments will shed new light on the  
5 ecophysiological effects of daytime and night-time warming during different seasons, and can  
6 be used to improve the performance of current land surface models.

7

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1 **Figure legends**

2 **Figure 1** Spatial patterns of the correlation between seasonal NDVI and corresponding daily  
3 maximum ( $T_{\max}$ ) or minimum temperatures ( $T_{\min}$ ) in the mid- and high- latitudes of the  
4 Northern Hemisphere during 1982-2011. (a), (c) and (e) are the spatial patterns of partial  
5 correlation coefficients between NDVI and  $T_{\max}$  during April-May (a), June-August (c) and  
6 September-October (e), respectively. The corresponding  $T_{\min}$ , precipitation and solar radiation  
7 are controlled for in the calculation. (b), (d) and (f) show the partial correlation coefficients  
8 between NDVI and  $T_{\min}$  during April-May (b), June-August (d) and September-October (f),  
9 while  $T_{\max}$ , precipitation and solar radiation are controlled for. The segment points  $\pm 0.49$ ,  
10  $\pm 0.38$ ,  $\pm 0.32$  and  $\pm 0.26$  correspond to 1%, 5%, 10% and 20% significant level of student's  
11 t-test.

12  
13 **Figure 2** Cumulative frequency distributions of the partial correlation between seasonal  
14 NDVI and daily maximum ( $T_{\max}$ ) or minimum temperatures ( $T_{\min}$ ). (a)-(b) are the cumulative  
15 frequency distributions of the partial coefficients between spring (April-May, red lines),  
16 summer (June-August, green lines) and autumn (September-October, blue lines) NDVI and  
17  $T_{\max}$  in boreal zone (a) and temperate regions (b), respectively. (c)-(d) show the cumulative  
18 frequency distributions of the partial coefficients between seasonal NDVI and  $T_{\min}$  in boreal  
19 zone and temperate regions. The cumulative distributions of positive and negative correlations  
20 are calculated separately. For positive correlations (right part of each subfigure), the  
21 frequency is cumulated from +1 while for negative correlations (left part of each subfigure),  
22 the frequency is cumulated from -1.

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**Figure 3** The responses of model simulated GPP to daily maximum temperature ( $T_{\max}$ ) or minimum temperature ( $T_{\min}$ ) in the mid- and high- latitudes of the Northern Hemisphere during 1982-2010. The color-coded patterns are derived from a two-dimensional color map in which the horizontal gradient represents the variations of partial correlation coefficients between GPP and  $T_{\max}$ , and the vertical gradient corresponds to the variations in the partial correlation coefficients between GPP and  $T_{\min}$ .

**Figure 4** The responses of model simulated LAI to daily maximum temperature ( $T_{\max}$ ) or minimum temperature ( $T_{\min}$ ) in the mid- and high- latitudes of the Northern Hemisphere during 1982-2010. The color-coded patterns are derived from a two-dimensional color map in which the horizontal gradient represents the variations of partial correlation coefficients between LAI and  $T_{\max}$ , and the vertical gradient corresponds to the variations in the partial correlation coefficients between LAI and  $T_{\min}$ .

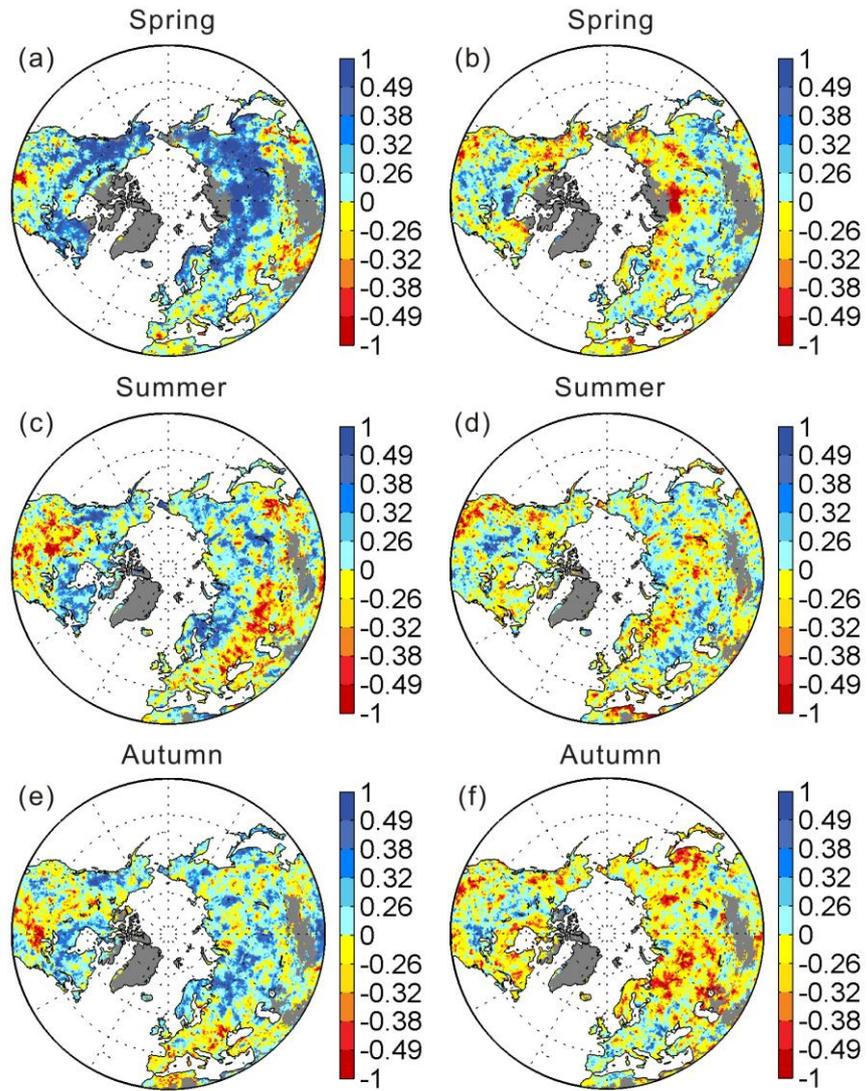
1 **Figure 1**

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Partial correlation coefficients  
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Partial correlation coefficients  
(NDVI and  $T_{min}$ )



1 **Figure 2**

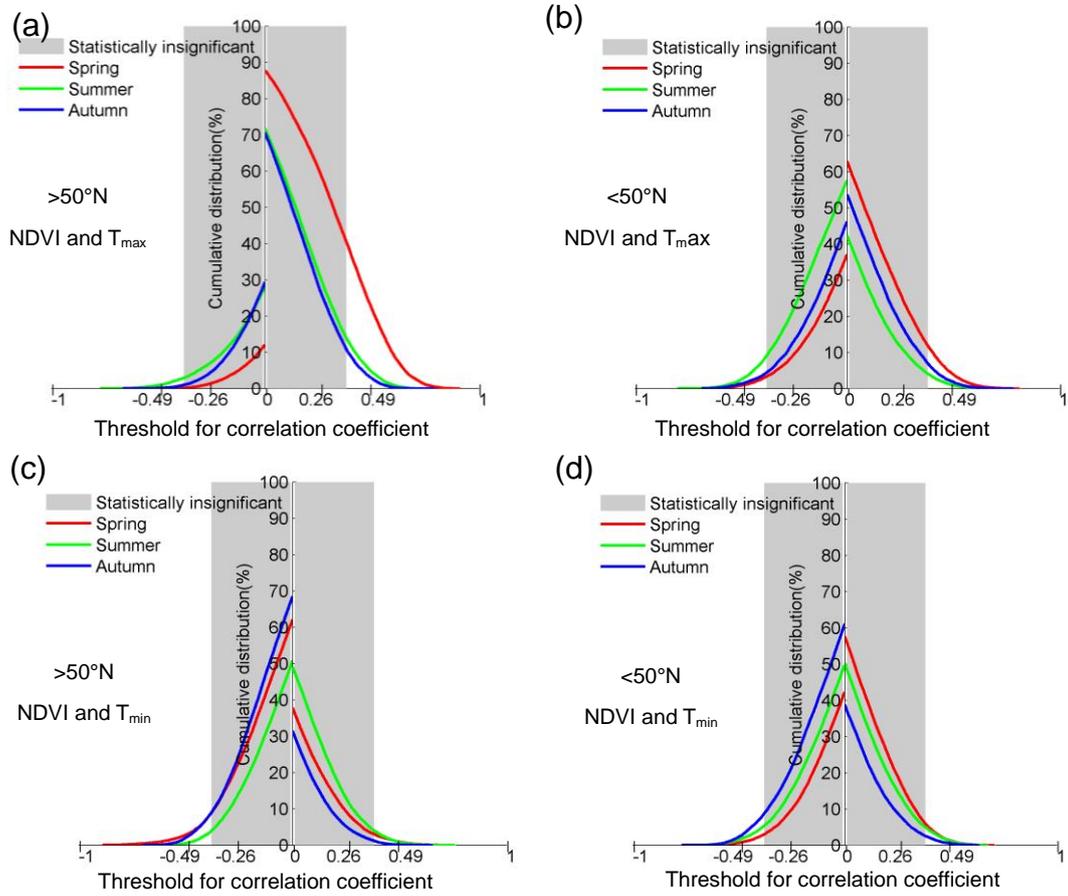
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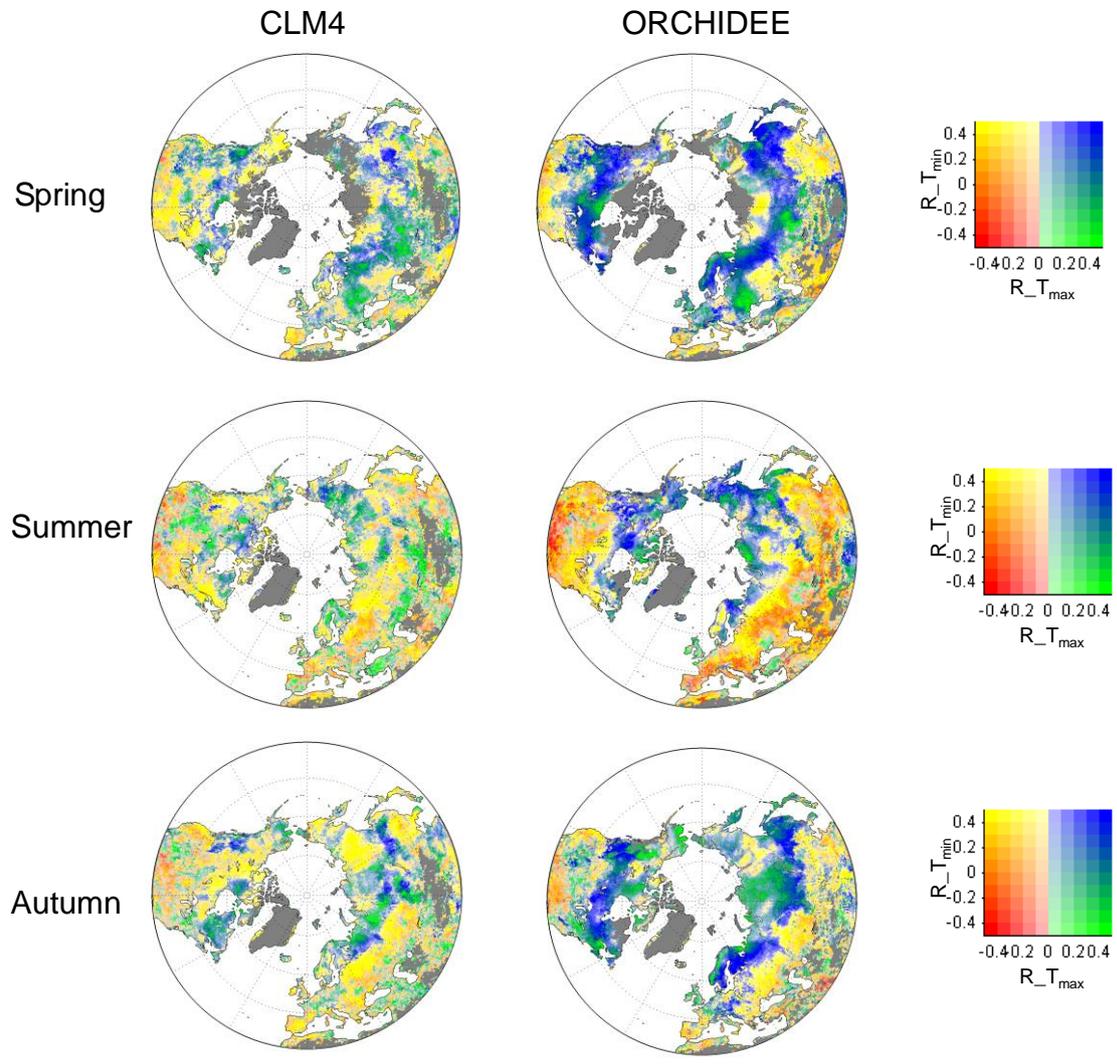
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1 **Figure 3**

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1 **Figure 4**

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