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Velocity of change in vegetation productivity over northern high latitudes

- 3 Mengtian Huang¹, Shilong Piao^{1,2}, Ivan A. Janssens³, Zaichun Zhu¹, Tao Wang², Donghai Wu¹,
- 4 Philippe Ciais^{1,4}, Ranga B. Myneni⁵, Marc Peaucelle^{4,6,7}, Shushi Peng¹, Hui Yang¹, Josep
- 5 Peñuelas^{6,7}

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- ¹ Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences,
- 8 Peking University, Beijing 100871, China.
- ⁹ Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100085, China.
- ³ Centre of Excellence PLECO (Plant and Vegetation Ecology), Department of Biology,
- 11 University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium.
- ⁴ Laboratoire des Sciences du Climat et de l'Environnement, CEA CNRS UVSQ, Gif-sur-Yvette
- 13 91190, France.
- ⁵ Department of Earth and Environment, Boston University, Boston, Massachusetts 02215,
- 15 USA.
- ⁶ CREAF, Cerdanyola del Vallès, Barcelona 08193, Catalonia, Spain.
- ⁷ CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, Barcelona 08193, Catalonia,
- 18 Spain.

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Warming is projected to increase the productivity of northern ecosystems¹⁻³. However, knowledge on whether the displacement of vegetation productivity isolines matches the northward motion of temperature isolines is still limited. Here, for the first time, we compared changes in the spatial patterns of vegetation productivity and temperature using the concept of velocity of change, which is defined as the ratio of temporal changes in a variable to the spatial gradient of the same variable, making it possible to express these two variables in the same unit of displacement per time⁴⁻⁹ (e.g. km vr⁻¹). Normalized Difference Vegetation Index (NDVI) data from 1982 to 2011 was used to calculate the velocity of vegetation productivity north of 50°N. Our results show that the average velocity for growing season (GS) NDVI (NDVIGS; 2.8±1.1 km yr⁻¹) is lower than that for GS mean temperature (T_{GS}; 5.4±1.0 km yr⁻¹). About 20% of the study area display larger velocities of NDVIGS than TGS, mainly in eastern Europe, northeastern and southern Siberia, and parts of western Canada. By comparison, in northern Europe, western and central Siberia, and northeastern Canada (52% of the study area), the NDVIGS velocity is less than half of T_{GS} velocity, indicating that the northward motion of productivity isolines is much slower than that of temperature isolines over the last 30 years. We tentatively attribute this mismatch between the velocities of vegetation productivity and temperature to the effects of limited resource availability and vegetation acclimation mechanisms. Analyses of the velocity of ecosystem productivity from ecosystem model simulations further suggested that limited nitrogen availability is a crucial obstacle for vegetation to track the warming trend.

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The Earth's climatic system is experiencing significant warming, which has raised concerns about the impacts on terrestrial ecosystems 10. In-situ observations, manipulative experiments, 45 as well as satellite-derived data have all pointed out that vegetation productivity is sensitive to 46

temperature change in northern high latitudes^{1,11-14}. 47

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Vegetation can adjust to climate change through relatively fast mechanisms (e.g. adjustment of phenology or physiology^{15,16}) and through slower mechanisms (e.g. phenotypic and genotypic adaptations, changes in community composition ¹⁶). If climate changes slowly and vegetation has ample time to adjust, it can be expected that warming would result in a northward shift of vegetation structure and function in the northern hemisphere. In reality, temperature acclimation and adaptation of plants¹⁷, as well as limited resource availability such as nitrogen¹⁸, may prevent vegetation productivity change from keeping the same rate as the rapid climate warming. To the contrary, CO₂ fertilization effects and regional nitrogen deposition may amplify the greening trend induced by warming temperature^{3,19}. Unfortunately, knowledge about the rate at which vegetation responds to ongoing temperature change is still limited. In particular, it is not known whether and to what extent change in the spatial displacement of vegetation productivity isolines during recent decades matches the northward motion of temperature isolines.

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The concept of velocity of change⁹ offers the opportunity to directly compare the ongoing change in the spatial patterns of temperature and productivity. This concept was first developed for climate impact research to compare the displacement rate of a forcing variable (e.g. temperature) with that of an impacted variable (e.g. the occurrence of a given species) by converting them into the same units^{4-9,20} (e.g. km yr⁻¹). The velocity of change in a geospatial variable is the ratio of its temporal change to its local geographical gradient^{5-7,21,22}. Imagine, for instance, that the mean spring temperature has increased by 0.3°C over 30 years. At the same location, a 1°C temperature spatial gradient is observed across a 100 km distance with a south-to-north decrease in temperature. The velocity of spring temperature change is then 1 km yr⁻¹ for this example (temporal trend of 0.3°C over 30 years, divided by the spatial gradient of 1°C over 100 km).

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In a similar manner, within the boundaries of a biome, we can calculate the velocity of change in vegetation productivity (also in km yr⁻¹). For each local cell, plant productivity responds to the changes in ambient environment condition, whether the responses are through changes in phenology or physiology of plant individuals (in-situ), or changes in community composition (e.g. shrub expansion). Such changes in productivity for each of the multiple pixels over a region eventually appear as the movement of productivity isolines at regional scale (Supplementary Figure 1a). In this case, the velocity of productivity change indicates a displacement in the isolines of this variable due to changes in productivity in response to climate change for multiple pixels over a certain region (Supplementary Figure 1b). In another word, the concept of velocity here quantifies how the spatial pattern of vegetation productivity changes in response to environmental changes during the study period, with different speeds and directions for each pixel. For a certain location with a south-to-north decrease in vegetation productivity, a northward velocity of vegetation productivity of 1 km yr⁻¹ over the past 30 years would indicate that the current productivity of a certain ecosystem has increased from its value 30 years ago to a higher value today equaling to the past productivity of another ecosystem which is 30 km (1 km yr⁻¹×30 years) south of the target one. The comparison between the velocities of change in vegetation productivity and temperature then makes it possible to identify if the motion of productivity isolines is in the same directions of that of temperature isolines, or / and if the displacement of productivity isolines is faster/slower than that of temperature isolines. Then we can address the question of whether and to what extent changes in the spatial pattern of vegetation productivity during recent decades have matched the displacement of temperature isolines (Supplementary Information S1.1).

In this study, we mapped for the first time the vector (both velocity and direction) of change in vegetation productivity calculated using satellite-derived long-term Normalized Difference Vegetation Index (NDVI). The NDVI dataset covers the period of 1982-2011 and was analyzed for velocity in the region north of 50° N, where vegetation productivity responds mainly to temperature changes^{23,24}. Productivity velocities were then compared to those of temperature change (see Methods). To minimize the covariate effects of other environmental variables, our analyses focused only on the overlap of natural ecosystems (defined following the International Geosphere-Biosphere Program; see Methods; Supplementary Figure 2) and ecosystems where productivity is temporally positively (p<0.1) correlated with temperature during the study period (see Methods; Supplementary Figure 3). This study area represents about 76% of the vegetated area (annual mean NDVI>0.1) over the northern high latitudes.

We first calculated the distribution of the velocities and their directions for the sum of the April to October growing season (GS) NDVI (NDVI_{GS}) and GS mean temperature (T_{GS}) over the last 30 years (see Methods). The average NDVI_{GS} velocity is 2.8±1.1 km yr⁻¹ over the study area. Large NDVI_{GS} velocities (>10 km yr⁻¹) are found in eastern Europe, northeastern and western Siberia, and low values (<1 km yr⁻¹) in central and eastern Canada as well as western Siberia (Fig. 1a). In 89% of the study area, the directions of NDVI_{GS} vectors are from regions with higher NDVI_{GS} values to those with lower values, with the majority of the study area (55%) showing a northward movement (Fig. 1c). On average, T_{GS} velocity over the study area (5.4±1.0 km yr⁻¹) is nearly twice the NDVI_{GS} velocity. The largest T_{GS} velocities (>10 km yr⁻¹) are

observed in northern central and eastern Siberia, parts of Europe, as well as eastern and northeastern Canada, whereas low values ($<1 \text{ km yr}^{-1}$) are found only in southwestern Canada (Fig. 1b). Northward T_{GS} vectors are observed in 71% of the study area (Fig. 1d).

Comparing the vectors of NDVI_{GS} and T_{GS} (see Methods), we found that, across the study area, 91% of the study area show a positive ratio between the velocities of projected NDVI_{GS} vectors and the velocities of T_{GS} vectors (V_N : V_T ratio) (blue color in Fig. 1e). This suggests that in these regions, vegetation productivity has tracked the direction of temperature change during the study period. Among these regions, about 98% of the area show positive trends in both NDVI_{GS} and T_{GS} , that is, vegetation productivity has increased where temperature warmed. Only a few regions in western Canada with positive V_N : V_T ratio show decreasing NDVI_{GS} as a result of decreasing T_{GS} during the study period (Supplementary Figure 4). Larger NDVI_{GS} velocities (projected along the T_{GS} velocities) than T_{GS} velocities occur in 20% of the whole study area, mainly in eastern Europe, northeastern and southern Siberia, as well as parts of western Canada (Fig. 1e). In about half of the study area, the V_N : V_T ratio is lower than 0.5, in particular northern Europe, central Siberia, and northeastern Canada. Similar results are also obtained when using different climate forcing datasets, when choosing different GS definitions (May to September or April to September), or when NDVI_{GS} velocities were compared with those of mean annual temperature (Supplementary Figure 5; see also Methods).

Overall, the largest V_N : V_T ratios are found in relatively warmer regions (Supplementary Figure 6; R=0.89, p<0.01). Several possible reasons may explain this phenomenon. First, the ubiquitous CO_2 fertilization effect, which can amplify the warming-induced positive trend of productivity³, is expected to be relatively stronger at higher temperature^{25,26}. Second, larger V_N : V_T ratios in warmer regions may arise from larger nitrogen availability, either from

increased soil nitrogen mineralization or from additional nitrogen deposited to ecosystems in most of the warmer temperate regions of the northern hemisphere^{27,28}. In addition, the lower $V_N:V_T$ ratios found in colder climates may be associated with background limitations induced from the presence of permafrost (Supplementary Figure 7). Permafrost constrains the development of roots, and slows down the decompositions of soil organic matter limiting mineral nitrogen and phosphorus availability for plants²⁹.

In general, vegetation productivity north of 50°N is mainly limited by two factors: growing season length and growing season maximum photosynthetic capacity^{24,30}. Growing season length is determined by the start of the growing season (SOS) and the end of the growing season (EOS), which are closely associated with temperature²³, while peak growing season photosynthetic capacity can be partly reflected by the maximum NDVI in the growing season (MOS), which is jointly controlled by nutrient availability and temperature for the study area³¹. Hence, we analyzed separately the vectors of NDVI-derived SOS, EOS, and MOS, respectively (see Methods), as shown in Fig. 2.

The average velocity of change in the SOS date during 1982-2011 is 3.6±1.0 km yr⁻¹ over the study area. Pronounced differences in both velocity and direction of SOS vectors can be seen between Eurasia and North America in Fig. 2a and 2d, respectively. The majority of Eurasia (74%) show northward SOS vectors (related to the advance in spring phenology), while only half of North America display northward SOS vectors (Fig. 2d). In Eurasia, the velocity of SOS vectors exceeds 5 km yr⁻¹ in 61% of the whole area, whereas in most of North America (73% of the continent area north of 50°N), it is lower than 5 km yr⁻¹ (Fig. 2a). The largest SOS velocities (>20 km yr⁻¹) are observed in northeastern Siberia. This area also experiences the largest (>10 km yr⁻¹) velocities of springtime (March to May, MAM) temperature increase

(Supplementary Figure 8a). In addition, we found that about one third of the study area shows larger velocities of SOS vectors (projected along the spatial gradient of spring temperature) than those of spring temperature vectors themselves (Fig. 2g). These regions include central Europe, central and southern Siberia, as well as parts of eastern and northwestern Canada. By contrast, in western and northeastern Siberia, the velocities of projected SOS vectors are smaller than those of the vectors of springtime temperature (ratio<0.5). Moreover, for 17% of the study area, mainly in Canada, the SOS vectors do not parallel the direction of temperature vectors (red color in Fig. 2g). In eastern and central Canada, a delayed SOS date occurs with warming, whereas in western Canada, an earlier SOS date occurs despite the cooling trend of spring temperature (Supplementary Figure 9a and 10a). Such mismatches may be attributed to changes in the relationship between heat requirement and chilling accumulation (the duration and/or sum of cold temperature during dormancy) due to changes in the late-winter and spring temperature³²⁻³⁴.

It has been reported that the temperature sensitivity of EOS is lower than that of SOS, because changes in EOS are co-limited by other factors than temperature^{31,35,36} (e.g., photoperiod and soil moisture). At first sight, our analysis of EOS velocities suggests the opposite result: the average EOS velocity across the study area (6.0±1.1 km yr⁻¹) is nearly twice the SOS velocity (3.6±1.0 km yr⁻¹) during 1982-2011. Nearly 60% of the study area display EOS velocities larger than 5 km yr⁻¹ (Fig. 2b). However, change in mean temperature from August to October displays a much higher average velocity (7.1±1.0 km yr⁻¹) than that in spring temperature (3.7±1.0 km yr⁻¹), rendering their average warming dependency more similar. In any case, the co-regulation of EOS by other factors likely explains the much more heterogeneous pattern of the directions of EOS vectors (Fig. 2e) than that of SOS vectors (Fig. 2d). Comparing EOS and August to October mean temperature vectors, we found that regions where the velocities of projected EOS

vectors exceed those of the original temperature vectors are located mainly in southern Siberia as well as in northeastern and southwestern Canada, accounting for 36% of the study area (Fig. 2h). By contrast, northeastern Siberia and eastern Canada experience very strong warming during August-October (Supplementary Figure 10b), but the EOS vectors in these regions show generally lower velocity than in southeastern Siberia (Fig. 2b), resulting in a smaller ratio (<0.5) of EOS to autumn temperature change velocities (Fig. 2h). In parts of central Siberia and western Canada, we even observe an advanced EOS date with warming temperature (red color in Fig. 2h). This mismatch between the vectors of EOS and temperature change may be partly explained by the decreased solar radiation in these regions³⁶. Since it has been suggested that increases in solar radiation suppress the accumulation of abscisic acid and subsequently slow the speed of leaf senescence³⁷, the decline in solar radiation may have resulted in advanced EOS dates despite the warming temperature.

On average, the northern high latitudes exhibit an average MOS velocity of 3.1±1.0 km yr⁻¹ over the past three decades, which is lower than that of summer (June to July) temperature (4.2±1.1 km yr⁻¹). MOS velocities larger than 10 km yr⁻¹ are found in eastern Europe, northeastern Siberia and northeastern Canada, while values lower than 1 km yr⁻¹ mainly appear in the southern part of central Siberia, as well as in central and eastern Canada (Fig. 2c). Comparison between the velocity of MOS vectors (projected along the spatial gradient of summer temperature) and that of summer temperature vectors (Fig. 2i) show that larger MOS than temperature change velocities mainly occur in eastern Europe, northeastern Siberia, as well as in western and northeastern Canada, accounting for one third of the area where changes in MOS have tracked the direction of the temperature change (blue color in Fig. 2i). In northwestern Europe and southern Siberia, however, MOS velocities are generally less than half of summer temperature velocities. Since northern ecosystems are strongly temperature-

limited², the slower velocities of projected MOS vectors compared to summer temperature velocities may be partly attributed to the fact that photosynthesis at the peak of the growing season is constrained because the low-temperature-induced nutrient limitations do not allow the development of dense canopies³⁸. Interestingly, we found larger MOS velocities in shrub and tundra ecosystems (3.4±1.0 km yr⁻¹ on average) (vegetation types from the International Geosphere-Biosphere Program; Supplementary Figure 2) than in other vegetation types. Also the ratio of velocities of projected MOS vectors to summer temperature velocities is highest in shrub and tundra (Supplementary Table 1). Warming-induced tall shrub and tree expansion³⁹ may be responsible for the larger MOS velocities in shrub and tundra than in other terrestrial ecosystems.

Land surface models are used to project future responses of ecosystems to climate change and to analyze the contribution of different driving factors⁴⁰. We therefore examined the vectors of change in vegetation productivity using simulated net primary productivity (NPP) from five process-based land surface models (CLM4.5, LPJG, OCN, ORCHIDEE, and VEGAS; see Methods and Supplementary Table 2). Our results show that the ensemble model-mean of change in annual NPP displays an average velocity of 4.0±1.3 km yr⁻¹ (±standard deviation across models). The highest NPP velocity values (>10 km yr⁻¹) are found in southern and northeastern Siberia (Supplementary Figure 11a). We next compared the velocities of simulated NPP with those of NDVI_{GS} after projecting both NPP and NDVI_{GS} vectors along the spatial gradient of T_{GS} (see Methods). The results show that, on average, about 60% of the study area (ranging from 47% to 70% across different models) show higher velocities of simulated NPP than of NDVI_{GS}. Further, we examined the NPP velocities using a satellite-derived terrestrial NPP product (GIMMS_{3g} NPP; see Methods), which display spatial patterns consistent with those of the NDVI_{GS} vectors (for both velocity and direction), albeit with generally lower

velocity across the study area (Supplementary Figure 12). Compared with the GIMMS_{3g} NPP, the model-simulated NPP produces larger velocity in about 71% (ranging from 61% to 81%) of the study area. This mismatch regarding the increase in productivity under warming between model- and satellite-based estimates may partly be explained by the limited availability of nitrogen in these regions⁴¹, which is suggested to prevent changes in vegetation productivity from adequately tracking the warming trend, but are not accounted for in some of the models⁴². Interestingly, we found that the two models with nitrogen limitations and nitrogen deposition taken into consideration (CLM4.5 and OCN) both produce lower NPP velocities (1.7±1.0 km yr⁻¹ and 2.0±1.1 km yr⁻¹ for CLM4.5 and OCN, respectively) than those without a coupled nitrogen cycle (3.5±1.0 km yr⁻¹, 2.9±1.1 km yr⁻¹ and 4.7±1.2 km yr⁻¹ for LPJG, ORCHIDEE and VEGAS, respectively) (Supplementary Table 3). Similar results are also observed for gross primary productivity (GPP; Supplementary Table 3 and Figure 13).

In summary, in this study we applied the concept of velocity to remotely sensed NDVI fields and compared the NDVI velocity to that of temperature in northern (predominantly temperature limited) ecosystems north of 50°N. The average velocity of change in NDVI_{GS} (2.8±1.1 km yr⁻¹) over the study area is only about half of that in T_{GS} (5.4±1.0 km yr⁻¹). A mismatch between the NDVI_{GS} and T_{GS} velocities suggests that the ratio of sensitivities of productivity to temperature across space and in time is not equal to one (Supplementary Information S2.1). Our analyses thus combined time and space and to some extent challenged the space-for-time substitution hypothesis⁴³ as applied in several studies using spatial gradients to back-cast temporal changes. Moreover, such a mismatch between productivity and temperature velocities suggests a disequilibrium in the plasticity of vegetation productivity changes to tail off with the spatial spread of warming. This may due to the prevalence of background spatial limitations by other factors limiting vegetation productivity such as soil moisture and nutrients¹⁸, which also

correspond to vegetation acclimation to the ongoing warming¹⁷, as well as the transient limitations in the rate of adjustment of plant response to the warming rate in different seasons. In addition, differences in the magnitudes of the SOS, EOS and MOS velocities suggest that the seasonal profile of vegetation growth has strongly re-shaped over time and that limitations may be expected in spring phenology not being able to track temperature moving northward (e.g. for photoperiod limitations, chilling requirements reasons³²⁻³⁴).

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Methods

Data. The monthly air temperature data set used in this study is the CRU TS 3.22 climate data set obtained from Climatic Research Unit (CRU) for the period January 1982 to December 2011 (http://www.cru.uea.ac.uk/cru/data/hrg/). We also used WATCH Forcing Data Methodology to ERA-Interim data with temporal resolution of 3 hour (WFDEI)⁴⁴. The third generation Global Inventory Monitoring and Modeling System Normalized Difference Vegetation Index (GIMMS NDVI_{3g}) data set from the Advanced Very High Resolution Radiometer (AVHRR) sensors was downloaded from http://ecocast.arc.nasa.gov/data/pub/gimms/3g.v0/. The data set has 15-day temporal frequency from July 1981 to December 2011 with a spatial resolution of 8 km⁴⁵. Only positive NDVI values from January 1982 to December 2011 were used in this study. We also used a 16-day NDVI datasets retrieved using observations from Terra Moderate Resolution Imaging Spectroradiometer (MODIS) (MODIS NDVI) from February 2000 to July 2012 with spatial resolutions of 1 km⁴⁶ to test the robustness of the analyses conducted with GIMMS NDVI_{3g} data. A 30-year (1982-2011) satellite-derived terrestrial net primary productivity (NPP) data set presented in a recent study⁴⁷, which was calculated using GIMMS leaf area index (LAI) and fraction of photosynthetically active radiation absorbed by the vegetation (FPAR) based on MODIS NPP algorithm⁴⁷, was also used. Note that the spatial structures of the error in the surfaces of NDVI and temperature may be different due to different approaches to obtain gridded datasets. For example, the NDVI differences between neighboring cells obtained from composite AVHRR images may be more contrasted than those of climate data being obtained by interpolation of station data or re-analysis with numerical weather prediction models. To reduce the effect of fine scale spatial structure in the errors on each surface, all the data have been regridded into a common 1°×1° grid. A mask is applied whereby grid cells where annual mean NDVI is less than 0.1 are excluded to remove areas with very low ecosystem productivity. Vegetation types defined following the International Geosphere-Biosphere Program based on a MODIS land cover classification (http://webmap.ornl.gov/wcsdown/wcsdown.jsp?dg_id=10011_1) were used to further remove hardly natural and non-natural vegetation lands.

Satellite-derived indexes of vegetation productivity. The maximum NDVI value at each bimonthly time step was used to calculate monthly NDVI in order to minimize the effects of atmospheric water vapor, non-volcanic aerosols and cloud-cover⁴⁵. The growing season (GS) NDVI (NDVI_{GS}) was calculated as the sum of monthly NDVI values from April to October. GS defined as May to September and April to September were also used for robustness test. Note that over the northern high latitudes, calculating NDVI_{GS} with a predefined period is to some extent challenging in the boreal regions because of the snow effect. Therefore, we calculated the percentage of the study area with possible snow effects using he quality flag information of GIMMS NDVI_{3g} datasets⁴⁵. To be specific, when regridding the original 8 km (\approx 1/12 degree) monthly data into a 1°×1° gridded monthly data, a 1°×1° pixel is considered to be affected by snow in this month if less than 70% pixels within a 12×12 pixel window have a flag value of 1 or 2 (good value). For each year, a pixel is then considered to be affected by snow if more than 2 months during the predefined growing season (e.g. April-October) is affected by snow. Finally, we defined regions with snow effects as pixels with more than 9 years showing snow

effects during the study period. The results show that regions affected by snow are mainly located in Alaska, northern Europe and parts of eastern Siberia, accounting for only 12% of the study area (red color in Supplementary Figure 14).

Two phenological indexes were derived from GIMMS NDVI_{3g} data set: the start of growing season (SOS, DOY) and the end of growing season (EOS, DOY). The SOS date was calculated as the averaged SOS date estimated by four different methods: Timesat, Spline, Hants and Polyfit⁴⁸⁻⁵⁰. The EOS date was obtained from the averaged EOS estimated by four different methods: Hants, Polyfit, Double Logistic and Piecewise Logistic³⁶. For each year during 1982-2011, the maximum NDVI of growing season (MOS) was calculated as the peak NDVI value among monthly NDVI values during the growing season, which was defined based on the month when the SOS and EOS date occurred.

Model-simulated ecosystem productivity. We used NPP and gross primary productivity (GPP) outputs from 1982 to 2011 from five process-based land surface models: CLM4.5, LPJG, OCN, ORCHIDEE, and VEGAS (see model list in Supplementary Table 2). All models were run based on the TRENDY inter-comparison protocol during the period 1901-2010 using the same observed climate drivers from CRU-NCEP Version 4 (http://dods.extra.cea.fr/data/p529viov/cruncep/), rising atmospheric CO₂ from the combination of ice core records and atmospheric observations, and land use change from the Hyde database (http://dgvm.ceh.ac.uk/node/21). NPP and GPP from all the five models were all resampled into 1°×1° grids.

The vector of change. The vector of change in a certain variable takes both velocity and direction into consideration. For each pixel, the velocity was defined as the ratio between the

30-year temporal trend and the spatial gradient in 30-year means^{4,6,9,51}. Temporal trend was calculated using least squares linear regression for each grid⁵¹. Spatial gradient was calculated using a 3×3 grid cell neighborhood based on the average maximum technique⁹. Following Loarie et al.⁹, to convert cell height in latitudinal degrees to km, we used 111.325 km degree⁻¹. To convert cell width in longitudinal degrees to km, we calculated $\cos\left(\frac{\pi}{180}y\right)$ 111.325, in which y is the latitude of the pixel in degrees. We also added a uniformly distributed random noise to each pixel to decrease the incidence of flat spatial gradients that cause infinite velocity values⁹. For temperature, a random noise from -0.05 to 0.05 °C was used; for NDVI_{GS} and the maximum NDVI value during growing season (MOS), a random noise from -0.005 to 0.005 was used; for the start / end of the growing season (SOS / EOS), a random noise from -0.05-0.05 DOY was used; for NPP / GPP, a random noise from -0.5-0.5 gC m⁻¹ yr⁻¹ was used. The direction of each vector was determined from the orientation of the spatial gradient, together with the direction of change in a particular variable⁴. For example, if temperature showed a positive trend during the study period, then the direction of temperature vector is towards areas that used to be cooler. Therefore, assuming a south-to-north decrease in temperature over the study area, then a northward (that is, along the spatial gradient) temperature vector indicates a warming temperature during the study period. Similarly, a northward NDVI_{GS} vector refers to an increase in NDVI_{GS} during the study period. A northward SOS vector is evidence for an earlier trend in SOS date, while for EOS, a northward vector is evidence for a delayed EOS date during the study period. A northward MOS vector is associated with a positive trend of MOS at the local pixel during the study period.

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We compared the velocity of change in NDVI_{GS} derived from GIMMS NDVI_{3g} with the one obtained from MODIS NDVI during 2001-2011. The processing of MODIS NDVI datasets is based on spectral bands that are specifically designed for vegetation monitoring and take state-

of-the-art navigation, atmospheric correction, reduced geometric distortions and improved radiometric sensitivity into consideration⁴⁶. MODIS NDVI is considered to be an improvement over the NDVI product derived from the AVHRR sensors^{46,52}, but it also has the disadvantage of shorter time span compared to GIMMS NDVI_{3g}. Generally, the NDVI_{GS} velocity from MODIS NDVI shows similar spatial pattern to that from GIMMS NDVI_{3g}, even though larger values of the former than the latter in parts of central, northern and northeastern Canada (Supplementary Figure 15).

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Analysis. This study covered regions where vegetation productivity was temporally significantly (p<0.1) correlated with temperature from 1982 to 2011. Assuming a linear relationship between vegetation productivity and temperature, the strength (correlation) of the linkage between the two variables was determined by the Pearson correlation coefficient between the time series of NDVI_{GS} and GS mean temperature, i.e., between the time series of the sum of monthly NDVI during April-October and the mean temperature during April-October. To compare the vectors of vegetation productivity and temperature velocities, for each grid cell, we calculated the ratio between the velocity of vegetation productivity (V_V) along the spatial gradient of temperature (V_V') and the velocity of temperature (V_T). Here V_V' was computed as the velocity of the vegetation vector after projecting it along the spatial gradient of temperature, which can expressed as $V_{V_I} = |V_V| \times \cos(|A_T - A_V|)$, where A_T and A_V is the vector angle (in radians) for metrics of temperature and vegetation productivity, respectively. The sign of the ratio between V_{V} and V_{T} was determined from the directions of both vectors. For a given pixel, a positive ratio is observed if the vector of change in vegetation productivity displays the same direction as the vector of temperature change, suggesting that change in the spatial pattern of vegetation productivity was directionally consistent with that of temperature. A negative ratio indicates that the directional change in the spatial patterns of the two variables were of opposite directions. The NDVI_{GS} vector was compared with the vector of GS mean temperature with different definitions of GS: April to October, May to September, and April to September. Comparisons of vector of NDVI_{GS} and that of mean annual temperature were also presented. Since the timing of vegetation phenology is associated with temperature of the preceding 0-3 months^{36,53}, here the vector of change in the SOS and EOS date were compared with that of change in mean temperature during March to May and August to October, respectively. The vector of change of MOS was compared with that of change in mean temperature during June to July. Note that since it has been well recognized that increasing spring temperature (i.e. positive trend of temperature) tends to result in an earlier SOS date (i.e. negative trend of SOS date) over most of northern ecosystems during the past three decades⁵⁴, regions where the change in vegetation productivity were consistent with warming trend refer to those with a negative trend in SOS date during the study period. The vectors of change in satellite-derived NPP, as well as model-simulated annual NPP and GPP were calculated using the same methods as calculating NDVI_{GS} vectors, and compared with the vector of change in GS (April to October) mean temperature.

References

- Elmendorf, S. C. et al. Plot-scale evidence of tundra vegetation change and links to
- recent summer warming. *Nat. Clim. Chang.* **2**, 453-457 (2012).
- Nemani, R. R. et al. Climate-driven increases in global terrestrial net primary
- production from 1982 to 1999. *Science* **300**,1560-1563 (2003).
- 215 Zhu, Z. et al. Greening of the Earth and its drivers. Nat Clim Chang 6, 791-795 (2016).
- 416 4 Ackerly, D. et al. The geography of climate change: implications for conservation
- biogeography. *Divers. Distrib.* **16**, 476-487 (2010).

- Burrows, M. T. *et al.* The pace of shifting climate in marine and terrestrial ecosystems.
- 419 *Science* **334**, 652-655 (2011).
- Burrows, M. T. et al. Geographical limits to species-range shifts are suggested by
- 421 climate velocity. *Nature* **507**, 492-495 (2014).
- Diffenbaugh, N. S. & Field C. B. Changes in ecologically critical terrestrial climate
- 423 conditions. *Science* **341**, 486-492 (2013)
- Dobrowski, S. Z. et al. The climate velocity of the contiguous United States during the
- 425 20th century. *Glob. Chang Biol.* **19**, 241-251 (2013).
- 426 9 Loarie, S. R. *et al.* The velocity of climate change. *Nature* **462**, 1052-1055 (2009).
- 427 10 Parry, M. L. Climate change 2007-impacts, adaptation and vulnerability: Working
- 428 group II contribution to the fourth assessment report of the IPCC, Cambridge University
- 429 Press (2007).
- Buitenwerf, R., Rose, L. & Higgins, S. I. Three decades of multi-dimensional change in
- 431 global leaf phenology. *Nat. Clim. Chang.* **5**, 364-368 (2015).
- Vitasse, Y., Porté, A. J., Kremer, A., Michalet, R. & Delzon, S. Responses of canopy
- duration to temperature changes in four temperate tree species: relative contributions of
- spring and autumn leaf phenology. *Oecologia* **161**, 187-198 (2009).
- 435 13 Wolkovich, E. M. et al. Warming experiments underpredict plant phenological
- responses to climate change. *Nature* **485**, 494-497 (2012).
- 437 14 Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J. & Hungate B. A. Responses of terrestrial
- ecosystems to temperature and precipitation change: a meta-analysis of experimental
- manipulation. *Glob. Chang Biol.* **17**, 927-942 (2011).

- 440 15 Peñuelas, J. & Filella, I. Responses to a warming world. *Science* **294**, 793-795 (2001).
- Penuelas, J. et al. Evidence of current impact of climate change on life: a walk from
- genes to the biosphere. *Glob. Chang Biol.* **19**, 2303-2338 (2013).
- Hikosaka, K., Ishikawa, K., Borjigidai, A., Muller, O. & Onoda, Y. Temperature
- acclimation of photosynthesis: mechanisms involved in the changes in temperature
- dependence of photosynthetic rate. J. Exp. Bot. 57, 291-302 (2006).
- 446 18 Way, D. A. & Oren, R. Differential responses to changes in growth temperature between
- trees from different functional groups and biomes: a review and synthesis of data. *Tree*
- 448 *Physiol.* **30**, 669-688 (2010).
- Thomas, R. Q., Canham, C. D., Weathers, K. C. & Goodale, C. L. Increased tree carbon
- storage in response to nitrogen deposition in the US. *Nat. Geosci.* **3**, 13-17 (2010).
- Sandel, B. et al. The influence of Late Quaternary climate-change velocity on species
- endemism. *Science* **334**, 660-664 (2011).
- Bi, J., Xu, L., Samanta, A., Zhu, Z. & Myneni, R. Divergent arctic-boreal vegetation
- changes between North America and Eurasia over the past 30 years. *Remote Sens.* 5,
- 455 2093-2112 (2013).
- LoPresti, A. et al. Rate and velocity of climate change caused by cumulative carbon
- 457 emissions. *Environ. Res. Lett.* **10**, 095001 (2015).
- Lucht, W. et al. Climatic control of the high-latitude vegetation greening trend and
- 459 Pinatubo effect. *Science* **296**, 1687-1689 (2002).
- 460 24 Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G. & Nemani, R. R. Increased plant
- growth in the northern high latitudes from 1981 to 1991. *Nature* **386**, 698-702 (1997).

- Hickler, T. et al. CO₂ fertilization in temperate FACE experiments not representative of
- boreal and tropical forests. *Glob. Chang Biol.* **14**, 1531-1542 (2008).
- Schimel, D., Stephens, B. B. & Fisher, J. B. Effect of increasing CO₂ on the terrestrial
- carbon cycle. Proc. Natl. Acad. Sci. U.S.A. **112**, 436-441 (2015).
- 466 27 Granath, G. et al. Photosynthetic performance in Sphagnum transplanted along a
- latitudinal nitrogen deposition gradient. *Oecologia* **159**, 705-715 (2009).
- Livingston, N., Guy, R., Sun, Z. & Ethier, G. The effects of nitrogen stress on the stable
- carbon isotope composition, productivity and water use efficiency of white spruce
- 470 (*Picea glauca* (Moench) Voss) seedlings. *Plant Cell Environ.* **22**, 281-289 (1999).
- Kimball, J. S. et al. Recent climate-driven increases in vegetation productivity for the
- western arctic: evidence of an acceleration of the northern terrestrial carbon cycle. *Earth*
- 473 *Interact.* **11**, 1-30 (2007).
- 474 30 Xia, J. et al. Joint control of terrestrial gross primary productivity by plant phenology
- and physiology. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 2788-2793 (2015).
- Forkel, M. et al. Codominant water control on global interannual variability and trends
- in land surface phenology and greenness. *Glob. Chang Biol.* **21**, 3414-3435 (2015).
- 478 32 Fu, Y. H. et al. Declining global warming effects on the phenology of spring leaf
- 479 unfolding. *Nature* **526**, 104-107 (2015).
- 480 33 Laube, J. et al. Chilling outweighs photoperiod in preventing precocious spring
- development. *Glob. Chang Biol.* **20**, 170-182 (2014).
- Zhang, X., Tarpley, D. & Sullivan, J. T. Diverse responses of vegetation phenology to a
- warming climate. *Geophys. Res. Lett.* **34**, L19405 (2007).

- Barichivich, J. et al. Large-scale variations in the vegetation growing season and annual
- cycle of atmospheric CO₂ at high northern latitudes from 1950 to 2011. *Glob. Chang*
- 486 *Biol.* **19**, 3167-3183 (2013).
- 487 36 Liu, Q. et al. Temperature, precipitation, and insolation effects on autumn vegetation
- phenology in temperate China. *Glob. Chang Biol.* **22**, 644-655 (2016).
- Gepstein, S. & Thimann, K. V. Changes in the abscisic acid content of oat leaves during
- 490 senescence. *Proc. Natl. Acad. Sci. U.S.A.* 77, 2050-2053 (1980).
- 491 38 Melillo, J. M. et al. Soil warming, carbon-nitrogen interactions, and forest carbon
- budgets. Proc. Natl. Acad. Sci. U.S.A. 108, 9508-9512 (2011).
- Frost, G. V. & Epstein, H. E. Tall shrub and tree expansion in Siberian tundra ecotones
- since the 1960s. *Glob. Chang Biol.* **20**, 1264-1277 (2014).
- 495 40 Sitch, S. et al. Evaluation of the terrestrial carbon cycle, future plant geography and
- 496 climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models
- 497 (DGVMs). Glob. Chang Biol. 14, 2015-2039 (2008).
- 498 41 Fisher, J. B., Badgley, G. & Blyth, E. Global nutrient limitation in terrestrial vegetation.
- 499 *Glob. Biogeochem. Cycles* **26**, GB1014 (2012).
- Likens G. Long-term Studies in Ecology (Springer, 1989).
- 501 43 Smith, N. G. & Dukes, J. S. Plant respiration and photosynthesis in global-scale models:
- incorporating acclimation to temperature and CO₂. Glob. Chang Biol. 19, 45-63 (2013).
- Weedon, G. P. et al. The WFDEI meteorological forcing data set: WATCH Forcing Data
- methodology applied to ERA-Interim reanalysis data. Water. Resour. Res. 50, 7505-
- 505 7514 (2014).

- 506 45 Pinzon, J. E. & Tucker, C. J. A non-stationary 1981–2012 AVHRR NDVI3g time series.
- 507 *Remote Sens.* **6**, 6929-6960 (2014).
- Huete, A. et al. Overview of the radiometric and biophysical performance of the MODIS
- vegetation indices. Remote Sens. Environ. 83, 195-213 (2002).
- 510 47 Smith, W. K. et al. Large divergence of satellite and Earth system model estimates of
- global terrestrial CO₂ fertilization. *Nat. Clim. Chang.* **6**, 306-310 (2016).
- 512 48 Cong, N. et al. Changes in satellite-derived spring vegetation green-up date and its
- linkage to climate in China from 1982 to 2010: a multimethod analysis. *Glob. Chang*
- *Biol.* **19**, 881-891 (2013).
- Piao, S., Fang, J., Zhou, L., Ciais, P. & Zhu, B. Variations in satellite-derived phenology
- in China's temperate vegetation. *Glob. Chang Biol.* **12**, 672-685 (2006).
- 517 50 White, M. A. *et al.* Intercomparison, interpretation, and assessment of spring phenology
- in North America estimated from remote sensing for 1982-2006. *Glob. Chang Biol.* **15**,
- 519 2335-2359 (2009).
- 520 51 Zheng, B., Chenu, K. & Chapman, S. C. Velocity of temperature and flowering time in
- wheat-assisting breeders to keep pace with climate change. *Glob. Chang Biol.* **22**, 921-
- 522 933 (2016).
- 523 Fensholt, R. & Proud, S. R. Evaluation of earth observation based global long term
- vegetation trends-Comparing GIMMS and MODIS global NDVI time series. *Remote*
- 525 Sens. Environ. 119, 131-147 (2012).
- 526 53 Piao, S. *et al.* Leaf onset in the northern hemisphere triggered by daytime temperature.
- 527 *Nat. Commun.* **6**, 6911 (2015).

528	Jeong, S., Ho, C. H., Gim, H. J. & Brown, M. E. Phenology shifts at start vs. end of
529	growing season in temperate vegetation over the Northern Hemisphere for the period
530	1982–2008. Glob. Chang Biol. 17, 2385-2399 (2011).
531	
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538	S.L.P. designed research; M.T.H. performed analysis; and all authors contributed to the
539	interpretation of the results and the writing of the paper.
540	
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544	addressed to S.L.P. (slpiao@pku.edu.cn)
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Figure Legends

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Figure 1 | The velocity of vegetation productivity (NDVIGS) and temperature (TGS) from 1982 to 2011 over northern high latitudes (north of 50°N). a, The spatial pattern of the velocity of the vector of change in NDVI_{GS}. b, The spatial pattern of the velocity of the vector of change in T_{GS}. c, The spatial pattern of the direction of the vector of change in NDVI_{GS}. d, The spatial pattern of the direction of the vector of change in T_{GS}. e, The comparison between velocity of NDVI_{GS} vector after projecting along the spatial gradient of T_{GS} and the velocity of T_{GS} vector (see Methods). The growing season is defined as from April to October. The velocity was calculated as the ratio between the 30-year temporal trend and the spatial gradient in 30year means (see Methods). The velocities shown in panel a and b are original velocities without projecting the NDVI_{GS} vectors along the temperature gradient. For panel c and d, 'N', 'NE', 'E', 'ES', 'S', 'SW', 'W' and 'NW' in the legend refer to 'North-ward', 'Northeast-ward', 'East-ward', 'Southeast-ward', 'South-ward', 'Southwest-ward', 'West-ward', and 'Northwestward', respectively. For panel e, the ratio between the velocity of NDVIGS along the spatial gradient of T_{GS} and the velocity of T_{GS} was calculated after projecting NDVI_{GS} vector along the spatial gradient of T_{GS} for each pixel (see Methods). A blue color (positive ratio) suggests that change in the spatial pattern of NDVIGS was directionally consistent with the direction of change in the spatial pattern of T_{GS}, while a red color (negative ratio) indicates that the former was inconsistent with the direction of the latter. Note that only gridded pixels covered by natural vegetation (defined following the International Geosphere-Biosphere Program based on a MODIS land cover classification; Supplementary Figure 2) with annual mean NDVI value larger than 0.1 are shown here.

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Figure 2 | The velocity (a-c) and direction (d-f) of the vector of change in vegetation phenology and physiology over the northern high latitudes (north of 50 °N) from 1982 to

2011 and comparison with the velocity of corresponding temperature metrics (g-i). Vegetation phenology is characterized by the start of the growing season (SOS) and end of the growing season (EOS); vegetation physiology is characterized by the maximum NDVI of growing season (MOS). For each pixel, the velocity for a certain variable was calculated as the ratio between the 30-year temporal trend and the spatial gradient in 30-year means for each index (see Methods). The velocities shown in panel a-c are original velocities without projecting the vegetation vectors along the temperature gradient. 'N', 'NE', 'E', 'ES', 'S', 'SW', 'W' and 'NW' in the legend for panel **d-f** refer to 'North-ward', 'Northeast-ward', 'East-ward', 'Southeast-ward', 'South-ward', 'Southwest-ward', 'West-ward', and 'Northwest-ward', respectively. For panel g-i, the ratio between the velocity of SOS/EOS/MOS along the spatial gradient of temperature and the velocity of temperature change was calculated after projecting the vectors of change in SOS/EOS/MOS along the spatial gradient of corresponding temperature metric for each pixel (see Methods). A blue color (positive ratio) suggests that change in the spatial pattern of SOS/EOS/MOS was directionally consistent with the direction of change in the spatial pattern of corresponding temperature metric, while a red color (negative ratio) indicates that the former was inconsistent with the direction of the latter. Pie chart of ratios shown in the spatial patterns is shown in the inset at bottom-left of panel g-i. Note that only gridded pixels covered by natural vegetation (defined following the International Geosphere-Biosphere Program based on a MODIS land cover classification; Supplementary Figure 2) with annual mean NDVI value larger than 0.1 are shown here.

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Figure 1

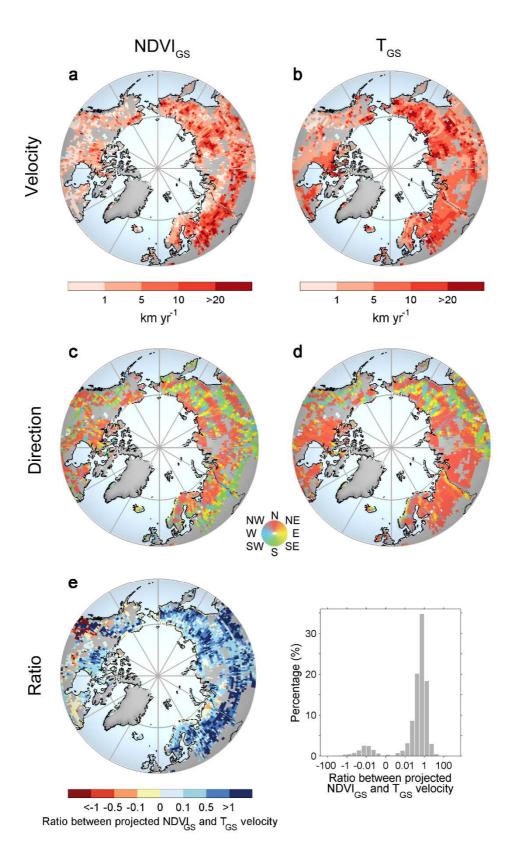


Figure 2

