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Terrestrial carbon cycle affected by non-uniform climate warming

Jianyang Xia[1], Jiquan Chen[2,3], Shilong Piao[4,5], Philippe Ciais[6], Yiqi Luo[1] and Shiqiang Wan[7]*

Feedbacks between the terrestrial carbon cycle and climate change could affect many ecosystem functions and services, such as food production, carbon sequestration and climate regulation. The rate of climate warming varies on diurnal and seasonal timescales. A synthesis of global air temperature data reveals a greater rate of warming in winter than in summer in northern mid and high latitudes, and the inverse pattern in some tropical regions. The data also reveal a decline in the diurnal temperature range over 51% of the global land area and an increase over only 13%, because night-time temperatures in most locations have risen faster than daytime temperatures. Analyses of satellite data, model simulations and *in situ* observations suggest that the impact of seasonal warming varies between regions. For example, spring warming has largely stimulated ecosystem productivity at latitudes between 30° and 90° N, but suppressed productivity in other regions. Contrasting impacts of day- and night-time warming on plant carbon gain and loss are apparent in many regions. We argue that ascertaining the effects of non-uniform climate warming on terrestrial ecosystems is a key challenge in carbon cycle research.

Temperature regulates almost all biogeochemical processes. Future climate warming will therefore have a profound effect on ecosystem functions and services such as carbon storage[1].

For example, climate warming influences terrestrial primary production directly by changing the leaf process intensity , but also indirectly by increasing soil nutrient mineralization[2–4], changing soil water availability[5], prolonging the growing season[6,7], shifting community structure[8] and altering disturbance regimes[9]. However, the rate of climate warming varies in magnitude between seasons and between day and night. Some regions, such as the west coast of subtropical South America[10], even experience cooling at certain points of the year. Temperatures have risen more quickly in winter than in summer at latitudes above 50° N, leading to a reduction in inter-seasonal differences in temperature at these high latitudes[11,12]. In contrast, summers have warmed more quickly than winters in some hot deserts, leading to an amplification of temperature seasonality in these regions[13]. Furthermore, the night has been shown to warm more quickly than the day in most areas of the world, leading to a reduction in the diurnal temperature range[14], although the opposite trend has been observed[14] and simulated[15] in some regions, such as the Mediterranean. This non-uniform rate of climate warming between seasons, regions and time of day may underpin regional differences in the response of ecosystem carbon cycling to warming, and thereby pose a great challenge to the prediction of future feedbacks between the climate and the carbon cycle.

To better understand how warming varies in space and time, we analysed global changes in seasonal mean and daily maximum and minimum temperatures using a long-term globally gridded database of air temperatures measured between 1948 and 2010[16]. The database was constructed by combining five global observation-based temperature data sets, and includes 3-hour near-surface meteorological data at a resolution of 1° × 1° (see details about the data set in Supplementary Text 1.1). We then analysed the partial correlations between satellite-based estimates of net primary production and seasonal or diurnal temperatures, and assess the effects of seasonal warming on carbon cycling with a process-oriented terrestrial biosphere model (CABLE)[17]. We also assessed the effects of increasing daily maximum and minimum temperatures on carbon-cycle processes using available model simulations from the Fifth Phase of the Coupled Model Intercomparison Project (CMIP5)[18]. Finally, we synthesized the latest findings on the impact of non-uniform climate warming on carbon cycling in terrestrial ecosystems.

Non-uniform trends in seasonal temperature change

The global land-surface annual mean air temperature increased at a rate of ~0.17 °C per decade between 1948 and 2010 (Fig. 1a), but has shown high variations among seasons (Fig. 1c–g). Overall, the air temperature has increased faster in spring (0.20 °C per decade) and winter (0.17 °C per decade) than in summer (0.13 °C per decade) or autumn (0.13 °C per decade) (Supplementary Fig. 1).

The trend in temperature seasonality, defined as the difference between the highest and lowest monthly mean temperature in each year, varied significantly between 1948 and 2010 (Fig. 1b). Latitudinal variations in warming in spring, summer, autumn and winter are shown in Fig. 1c–g. It is clear that the strongest rates of spring and winter warming (that exceed 0.30 °C per decade) have occurred more frequently at latitudes of 30–90° N. However, no clear latitudinal pattern was found for the summer or autumn warming (Fig. 1c–g; Supplementary Fig. 2). As a consequence, the temperature seasonality has diminished over time at mid to high latitudes from 30 to 90° N in the Northern Hemisphere[11] (Fig. 1b). Although the distributions of warming rates were relatively similar among

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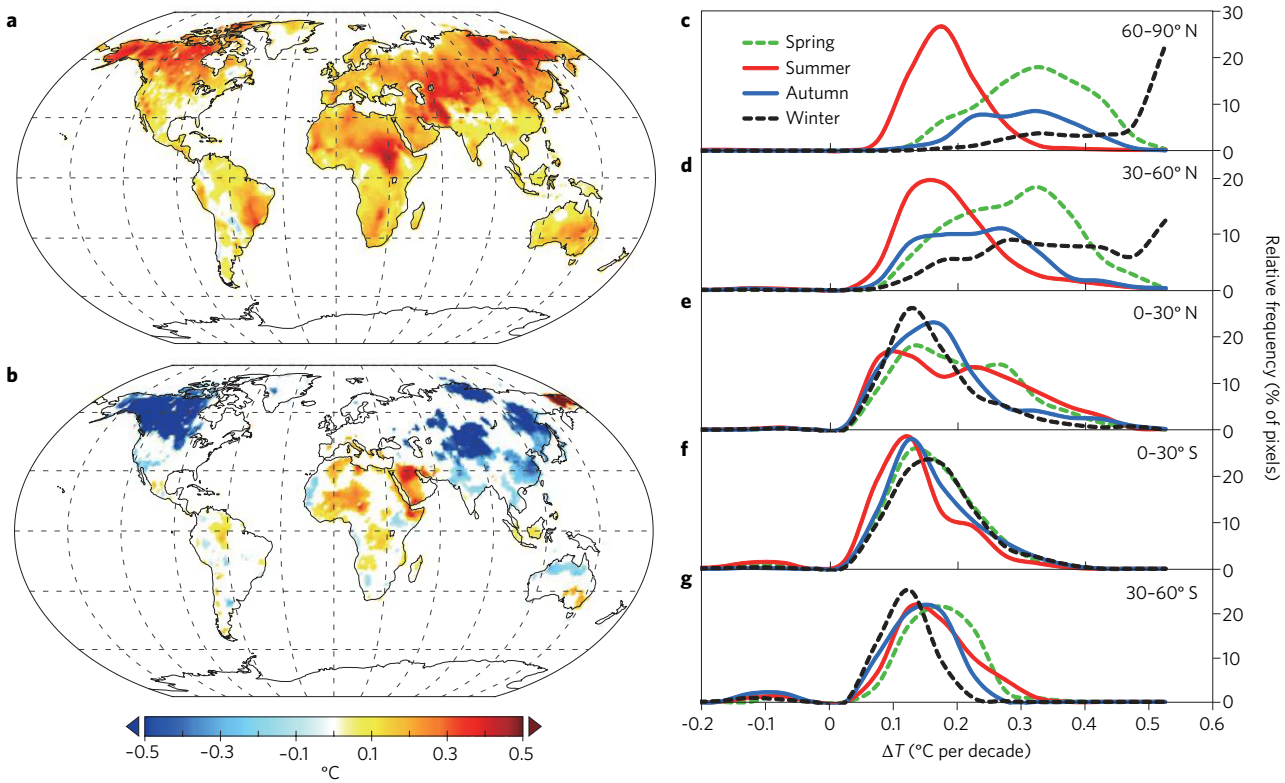

Figure 1 | Global trends of seasonal warming from 1948–2010. The changing trends (°C per decade) for each 1° × 1° latitude–longitude grid cell for **a**, annual mean air temperature and **b**, annual temperature range. **c**–**g**, The frequency of grid cells along seasonal trends in temperature (*T*) at 30° latitude intervals. The temperature trends were analysed with a linear regression model and an F-test was applied to test its significance (see Supplementary Text 1.1). If the *P* value for a grid cell was >0.1, we determined that the temperature change in that grid was insignificant and set its rate of temperature change as 0.

seasons at low latitudes (Fig. 1e,f), the temperature seasonality was amplified in some tropical regions (Supplementary Fig. 2), including in Africa and the Middle East (Fig. 1b).

Non-uniform trends in diurnal temperature change

The global daily minimum temperature increased at a rate of 0.16 °C per decade between 1948 and 2010, which is slightly faster than the rise in daily maximum temperature of 0.15 °C per decade (Fig. 2a, b). Both of these changes varied greatly across the globe. The magnitude of the rise in daily minimum temperature grew between 30° N and the high latitudes. The magnitude of the rise in the daily maximum temperature did not show any clear latitudinal trends, except for a decline between 50° and 90° N (Fig. 2d).

Between 1948 and 2010, the reduction in the diurnal temperature range ($P < 0.10$), that is, the difference between daily maximum and minimum temperature, was widespread throughout the world (51% of global land area). This decline was particularly pronounced in East Asia, the US, Colombia and northern Australia (Fig. 2c). Along latitudes, the largest reduction in the diurnal temperature range occurred at 60–90° N (Fig. 2d). Over the same time period, a significant increase in the diurnal temperature range was detected over 13% of the global land area ($P < 0.10$; Fig. 2c). For example, the diurnal temperature range increased in eastern Canada, and in some regions in western Asia, northern and central Africa, and southwestern Australia (Fig. 2c).

Direct and legacy effects of seasonal warming

Temperature change can influence the terrestrial carbon cycle by directly altering specific ecological processes in each season (Fig. 3). Spring warming advances the onset of leaf unfolding and associated activities, which, in turn, results in an earlier start of the growing season in most non-agricultural ecosystems[7,19,20]. That warming has hastened the arrival of spring growth, and so increased carbon uptake during spring, is supported by evidence from several studies (Figs 3a and 4).

Summer warming has a potentially positive effect on both terrestrial gross primary productivity and respiration (Fig. 3b), but the net effect on the ecosystem carbon balance may depend on the co-varying negative effects of water limitations at higher temperatures. For example, summer warming has had a positive impact on net primary productivity in most types of ecosystems, even with water limitations, according to several meta-analyses of experimental studies[21,22]. However, in arid and semi-arid grassland where soil water availability frequently falls below a critical threshold, summer warming itself could negatively affect net primary productivity by reducing soil moisture[23] (Fig. 3b).

Autumn warming seems to be more important for enhancing litter decomposition and has no clear influence on photosynthesis, probably due to the photoperiod limitation during this season[24]. As a consequence, autumn warming is usually found to reduce net ecosystem productivity in most northern terrestrial ecosystems[25], such as the boreal forest[26] (Fig. 3c).

Winter warming, especially at high latitudes in the Northern Hemisphere (Fig. 1c), is assumed to reduce snow cover and exacerbate soil freezing. This may increase the mortality of fine roots and thus contribute to the enhanced leaching loss of soil carbon and nitrogen from temperate forest[27] and tundra[28] as well as lowered winter soil respiration in an evergreen coniferous forest[29] (Fig. 3d). In temperate grasslands and forests, winter warming is also expected to raise the risks of plant damage by triggering disturbances such as frost injury and the outbreak of insect pests[30].

The warming within a season also indirectly affects ecological processes in the seasons that follow, known as the 'carry-over' or 'legacy' effect (Fig. 3), through regulating the phenology[31] and/

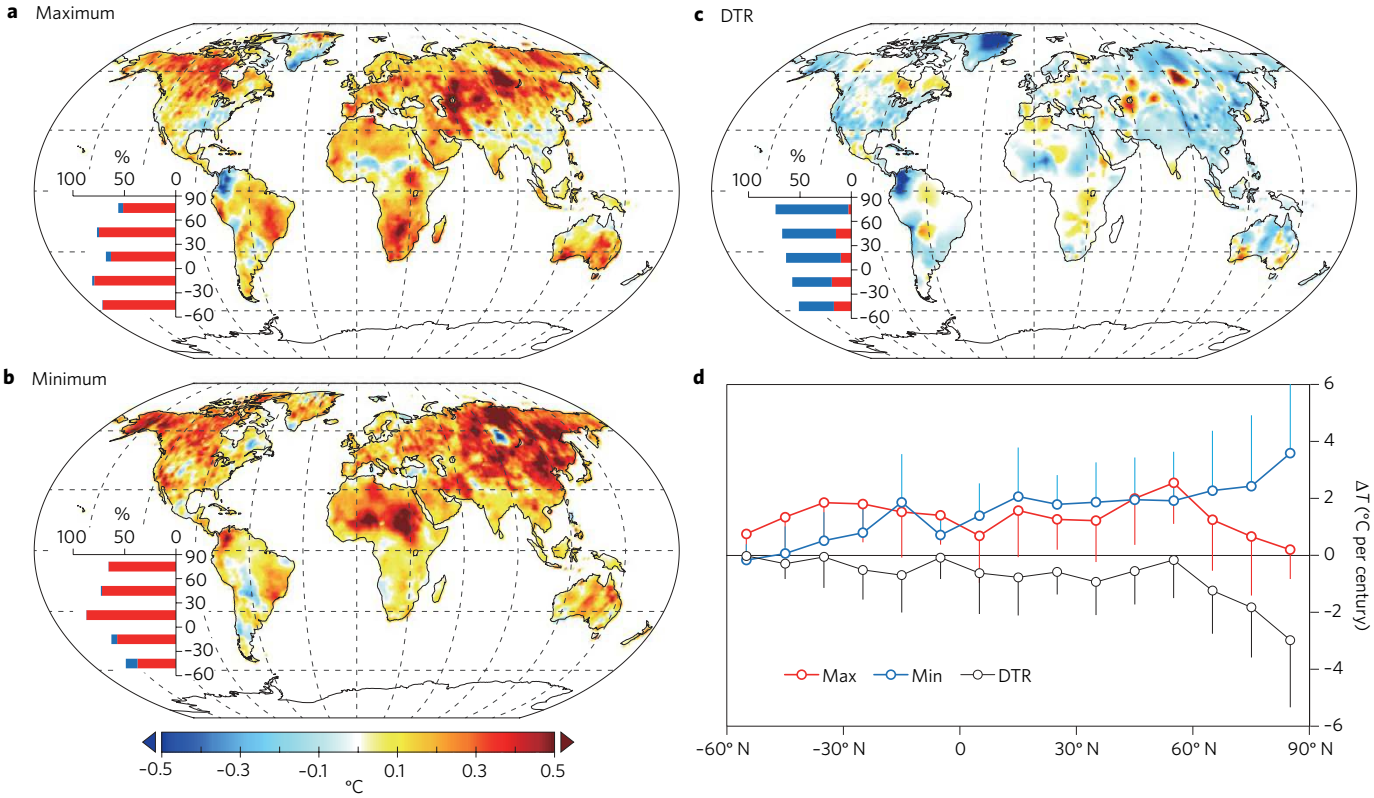

Figure 2 | Global trends of diurnal warming from 1948–2010. a–c, The changing trends (°C per decade) for each 1° × 1° latitude–longitude grid cell for mean daily maximum (**a**) and minimum (**b**) air temperature and mean diurnal temperature range (DTR; **c**). The insets in **a–c** show the frequency distribution of the proportion of land grids (%) with positive (red bars) and negative (blue bars) temperature trends from 60° S (lower limit of the vertical axis) to 90° N (upper limit) with a 30° interval. **d**, The area-weighing rates of temperature change (ΔT) along latitudes with a 10° interval (bars represent the standard deviation).

or availability of nutrients[32] and water[33,34]. Accelerated snowmelt by winter warming can generate opposite legacy effects on carbon processes in spring and summer[35]. Specifically, quicker snowmelt can lead to an earlier onset of photosynthesis in spring and a longer growing season and, consequently, a longer time period for net carbon uptake[7], but can also restrain fine root growth and the activity of soil microbes, and thus suppress nitrogen mineralization[36] and nitrogen-limited plant growth in the summer[37]. Similarly, the impacts of summer warming on plant growth and primary production will carry over into other seasons. For example, the positive effect of summer warming on net primary productivity in summer in wet regions can stimulate the microbial activities and litter decomposition for the rest of the year[28]. However, in dry regions, such as the Mediterranean and southern temperate regions, summer warming and associated drought events can decrease plant growth and litter decomposition in the subsequent winter[38]. Thus, season-specific warming can bring unexpected consequences on annual timescales. For instance, the positive impacts of winter–spring warming on ecosystem carbon sequestration through advancing plant phenology can be weakened or cancelled out by the stimulation of respiration by summer–autumn warming[25,26,39].

Spatial variations in the impact of seasonal warming

The spatial variability of trends in temperature seasonality (Fig. 1b) suggests that seasonal non-uniform warming will probably gen-erate different impacts on the C cycles in different regions of the world. We performed partial correlation analyses between seasonal mean temperatures and net primary productivity observations derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA's Terra and Aqua satellites (more details in Supplementary Text 1.2). The results showed that warming in each season had uneven impacts on net primary productivity among the ecosystems (Fig. 5a–d). During the short period of 11 years, spring warming was more likely to affect net primary productivity positively at latitudes from 30° to 90° N, but had more negative impacts at other latitudes (Fig. 5a). The dependency of net primary productivity on summer temperature is found to be positive at high latitudes in the Northern Hemisphere (60–90° N), but mostly negative in other regions, especially in the Mediterranean regions and the eastern US (Fig. 5b). Autumn temperatures had more positive than negative effects on net primary productivity at latitudes of 30–60° in both hemispheres, especially in the southwestern US, but had more negative impacts at other latitudes (Fig. 5c). Winter warming positively affected net primary productivity at latitudes of 30–60° S and 30–60° N, but had more negative influences in other regions, especially in Africa (Fig. 5d). These results, in combination with the global trends in temperature seasonality (Fig. 1b), indicate that the responses of the terrestrial carbon cycle to climate warming in different regions are dominated by different seasons.

To explore the sensitivity of net ecosystem productivity to warming in each season, we conducted a 2 °C warming simulation experiment with the CABLE model[17]. There were five simulations in the experiment, including one reference simulation with realistic climate forcing and four warming simulations, in which air temperatures were uniformly warmed by 2 °C in each season globally. If the simulated net ecosystem productivity increased or decreased as a result of warming in a given season, it was defined as the dominating season of the positive or negative warming effect. For example, in Alaska and western Canada, warming in different seasons all increased net ecosystem productivity, and the positive effect was

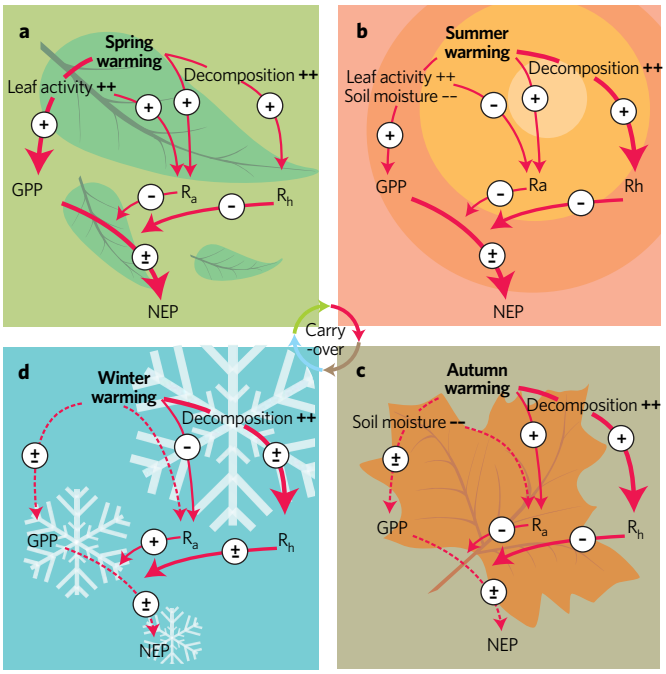

Figure 3 | Direct warming effects on the terrestrial carbon cycle in each season. Ecological processes affecting net primary productivity (NPP), gross primary productivity (GPP), autotrophic (R_a) and heterotrophic (R_h) respiration, and net ecosystem productivity (NEP) under climate warming in spring (**a**), summer (**b**), autumn (**c**) and winter (**d**) are illustrated. The solid and dotted lines represent the direct and indirect effects of warming on the carbon cycle, respectively.

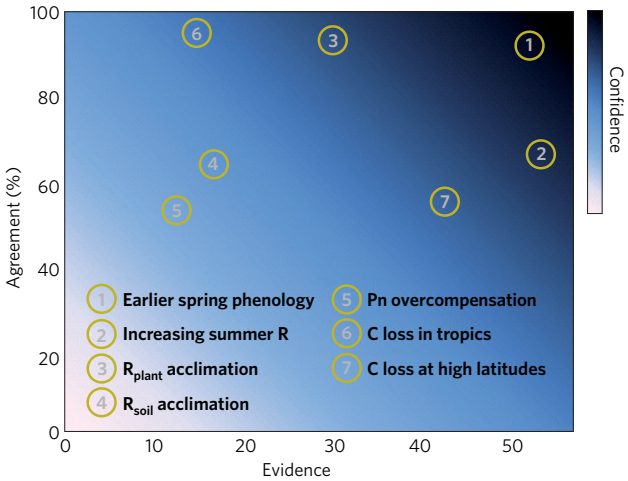

Figure 4 | Evidence, agreement and thus confidence of the selected warming-related carbon responses. 'Evidence' is the number of studies we found, and 'agreement' relates to the percentage of evidence that supports the given warming response. The increasing strength of shading towards the top-right corner indicates an increase in confidence. Data was obtained by a comprehensive literature search (see Supplementary Text 1). R, respiration; R_{plant}, plant respiration; R_{soil}, soil respiration; Pn, photosynthesis; C, carbon.

largest under winter warming (Supplementary Fig. 3) — and so winter was defined as the dominating season for the positive warming effect in this region (see Supplementary Text 1.3). We found that the positive effects of climate warming on net ecosystem productivity were dominated by spring warming at latitudes of 30–60° S (26% land grid cells), but by summer warming at higher latitudes of 60–90° N (41% land grid cells) (Fig. 5e and Supplementary Fig. 3). Autumn warming dominated the positive warming effects in northern Africa, whereas winter warming dominated in western Europe and the eastern US (Fig. 5e). The negative warming effect was dominated by summer warming in most regions from 60° S to 60° N (41% land grid cells; Fig. 5f). These results suggest that the prediction of future climate–carbon-cycle feedback relies largely on our understanding of how each season contributes to both temperature seasonality and annual carbon cycle responses.

The uneven trends in the seasonality of warming among regions (Fig. 1b) and the different response of carbon fluxes to seasonally distinct warming (Fig. 5) highlight the importance of studying the specific carbon responses to the shifting temperature seasonality by ecosystem type. At mid and high latitudes in the Northern Hemisphere, we found positive dependences of net primary productivity on spring temperatures in many regions, suggesting that spring warming may play an important role in enhancing ecosystem carbon uptake as temperature seasonality diminishes (Fig. 1b). Our synthesis further indicates a large disagreement among previous findings about the impact of warming at high latitudes (Fig. 4), which could be ascribed to several causes. First, vegetation seasonality can be affected differently by the warming in regions at high latitudes. For example, there is a significant trend towards earlier vegetation green-up in the spring in Eurasia, but North America exhibits significantly delayed vegetation senescence[6,25]. These findings infer that the contributions of an extended vegetation growing season to carbon cycling varies among regions (more significant greening patterns[40] and larger carbon sinks[41] in Eurasia than in North America). Second, geographical shifts of vegetation, as important drivers for changes in vegetation seasonality, have been found to positively[42] or negatively[43] influence vegetation carbon stocks in different regions at high latitudes. Third, the accelerated thawing of peatland permafrost with climate warming is expected to partially offset carbon sinks at high latitudes[44,45] and may turn it towards a net carbon source in the future[46]. However, there is widespread disagreement about the fate of permafrost carbon among the current generation of earth system models[47], suggesting that more research efforts are needed on the permafrost climate–carbon-cycle feedback.

At low latitudes, previous studies (Fig. 4) and our simulation results with the CABLE model (Fig. 5f) yield a consensus of carbon loss with the amplification of temperature seasonality. It is usually explained by the large-scale 'dieback' of tropical rainforests[48,49] or reduced odds of success for plant thermal adaptation to extremely high temperatures[50] under summer and autumn warming. However, the evidence from tropical regions is so scarce that our confidence on tropical carbon responses to the seasonal non-uniform warming remains relatively low (Fig. 4). Evidence from the ectotherm databases[51,52] and evolutionary modelling simulations[50] has shown that species in temperate ecosystems have broader thermal ranges than those in the tropics. Abiotic factors such as complex topography can provide a plant community with a spatial buffer against climate change[53,54], suggesting that mountainous ecosystems may have a higher resilience to climate warming than other systems[53,55].

Differential impact of day and night warming

Biological and ecological processes modulating the ecosystem carbon cycle carry different weights during the day and night. Plant species, especially C_3 and C_4 forms, take up carbon during the daytime through photosynthesis, with 30–80% of the carbon gained returning back to the atmosphere through respiration during the following night[56]. As a consequence, day and night warming will impact plant growth differently[57–60]. Daytime warming can enhance plant carbon uptake by increasing the temperature closer to its optimum for photosynthesis, but it can also inhibit plant growth if the temperature exceeds that optimal value. Because night time is solely dominated

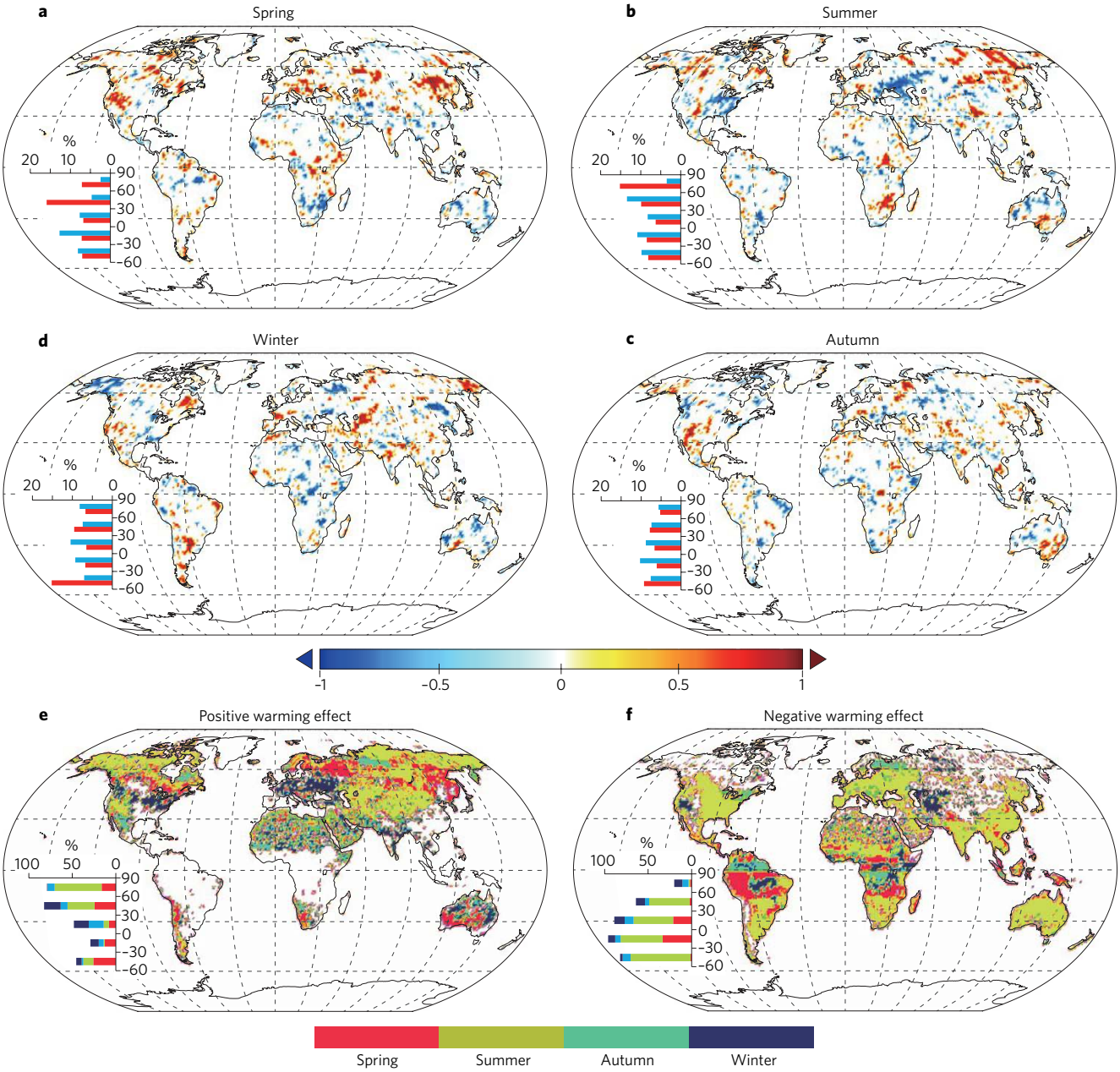

Figure 5 | Satellite-based and model-simulated impacts of seasonal warming on productivity. a–d, Partial correlation between net primary productivity and mean spring (**a**), summer (**b**), autumn (**c**) and winter (**d**) temperatures during 2000–2010. In evaluating the relationships between net primary productivity and mean temperatures of a given season (for example, spring), the mean temperatures in the other three seasons (for example, summer, autumn and winter) were treated as covariates. **e**,**f**, The dominating season in modelled positive (**e**) and negative (**f**) warming effects on net ecosystem productivity by the CABLE model. The insets in **a–d** show the relative frequency (%) distribution of positive (red bars) and negative (blue bars) contributions of seasonal temperatures to net primary productivity variation along the latitudes from 60° S (bottom) to 90° N (top) with a 30° interval. The insets in **e** and **f** show the relative frequency (%) of each season in dominating the positive and negative warming effects.

by respiration, warming at night will, in principle, elevate carbon loss. However, plant respiration may adapt or acclimate to higher temperatures and partially offset night-warming-induced CO_2 losses through respiration[61,62].

Although our confidence in the differential effects of day and night warming on ecosystem carbon loss is relatively high (Fig. 4), it seems to depend strongly on a series of processes with varying timescales[63], such as seasonal moisture stress and decadal vegetation change. As photosynthetic sugars flow towards the roots by transpiration in the daytime, but out of the roots during hydraulic redistribution at night, it has been hypothesized that the availability of root-derived substrate for soil microbe growth is low during the day but high at night[64]. As a result, even though the rate of rhizodeposition may be faster during daytime than at night, the microbes in the rhizosphere would be more active at night than during the day[64]. Thus, day and night warming would produce different impacts on soil microbial activities and, therefore, heterotrophic respiration. Evidence from a temperate steppe has shown that night but not day warming shifts the strategy of soil microbial carbon utilization, by reducing the relative proportion of total bacteria and arbuscular mycorrhizal fungi, and the associated use potential of amines, amino acids, polymers and root exudates[65].

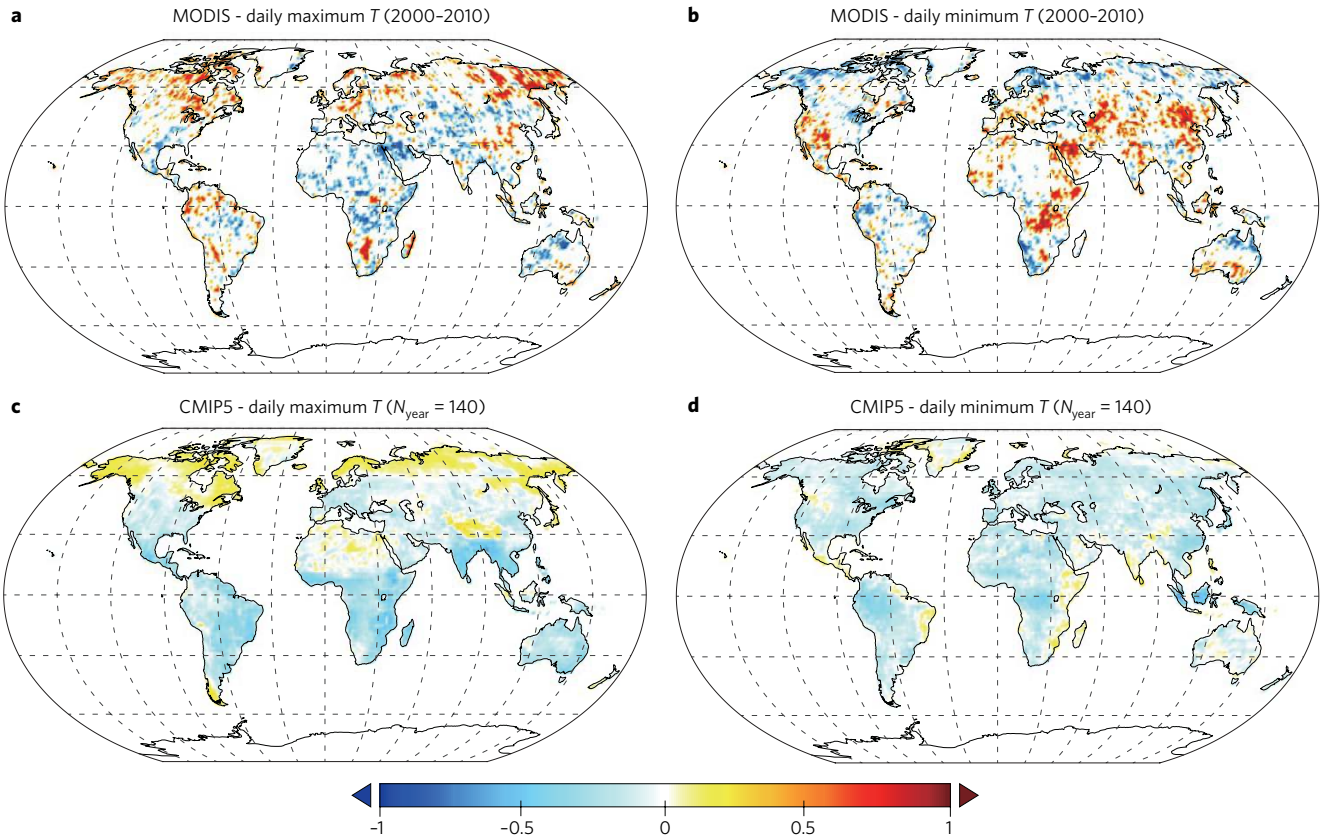

Figure 6 | Satellite-based and model-simulated impacts of diurnal warming on productivity. Partial correlation between net primary productivity and mean daily maximum and minimum temperatures (T) from MODIS satellite-based data during 2000–2010 (**a**,**b**) and the model-simulated data over 140 years (N_{year} = 140) after the pre-industrial condition (**c**,**d**). In evaluating the relationships between net primary productivity and the mean daily maximal temperature, daily minimal temperature was considered as covariate and vice versa (Supplementary Text 1.2). The results in **c** and **d** were averages of seven Earth system models in the CMIP5 experiment 5.4/5.5 (Supplementary Text 1.4). Results from each model can be found in Supplementary Fig. 5.

The processes of photosynthesis, respiration and growth are thought to be tightly linked[66]. Daytime warming alters net photosynthesis, which supplies the plant with substrates for respiration at night. Night warming, however, not only affects night-time plant respiration, but also may stimulate compensatory photosynthesis during the following day by depletion of leaf carbohydrates at night. Evidence supporting this hypothesis has been recently reported in both greenhouse[56] and field[60,67] experiments. However, it is unclear if the phenomenon of 'photosynthesis over-compensation' under nocturnal climate warming[60] exists widely in all ecosystems (Fig. 4). For example, no compensatory effect was found between respiration and photosynthesis under nocturnal warming in a Mediterranean grassland[68]. In fact, the dynamic of night-time plant respiration depends not only on carbon substrate from daytime photosynthesis, but also on other processes such as phloem loading[69]. It also remains unclear as to what extent carbon 'source activity' (that is, photosynthesis) is limited by 'sink activity' (that is, growth) within plants[66,70,71]. Multiple lines of evidence, such as a weak interannual relationship between eddy-covariance-derived gross ecosystem photosynthesis and tree ring width[72], increase in carbon concentration in plant organs under water deficit[70], and more limitations of alpine and arctic tree growth by cell division than photosynthesis[66], have suggested uncoupling between carbon source and sink activities. Although the diurnal rhythm of the rhizosphere community around the active uptake zone of roots could be important in controlling plant–microbe interactions[64], it remains unexplained how this mechanism regulates the response of ecosystem carbon cycling to diurnal non-uniform climate warming.

Spatial variations in the impact of diurnal warming

The shift in the terrestrial carbon cycle with the changing diurnal temperature range is determined by its response to changes in daily maximum and minimum temperatures. Consistent with a recent analysis on vegetation greenness[59], the partial correlation analyses between satellite-derived net primary productivity and daily maxi-mum and minimum temperatures showed contrasting effects of day and night warming in many regions over a short period of 11 years (Fig. 6a,b). For example, net primary productivity increased with daytime warming in most areas of tundra and boreal forests, but decreased in most grasslands and deserts (Fig. 6a). In contrast, grassland and desert primary production rose with night warm-ing, but declined in other regions (Fig. 6b). However, the depend-ence of annual primary productivity on the annual mean diurnal temperature range was insignificant in most regions of the world (Supplementary Fig. 4).

To examine whether the spatial patterns of day and night impacts have been well represented in the current generation of earth system models, we analysed the stimulated results from seven models in Experiment 5.4/5.5 of the Fifth Phase of the Coupled Model Intercomparison Project (CMIP5)[18] (see Supplementary Text 1.4 and Fig. 5). We found that the ensemble average of all model simulations captured the global pattern of day warming impact very well in comparison to the results from the observations (Fig. 6a), except in northern Africa and South America (Fig. 6c) — but they did not capture the positive impacts of night warming in dry regions such as the temperate grassland in North America and Eurasia (Fig. 6d). The spatial pattern of the day warming effect was better simulated by the

CESM1-BGC than by other models, and that of night warming effect was captured relatively well by the CESM1-BGC and IPSL-CM5A-LR models (Supplementary Table 1 and Fig. 5). We suggest that more attention should be paid to the functional response of carbon-related processes to changes in maximum and minimum day and night temperatures in the current generation of Earth system models.

Further research efforts are needed to explore new mechanisms controlling the spatial variability of the diurnal warming impacts on terrestrial carbon cycling. As shown by palaeoclimate research[73], the rapid rise in maximum temperature, for example in Canada, central Asia and southern Africa (Fig. 5a), may exceed the thermal tolerance of some local species and put them at risk of extinction. In some cases, photosynthesis is able to adjust to a new thermal regime, and operate more effectively at higher temperatures[56,74]. However, the extent to which the thermal optimum of ecosystem-level photosynthesis can shift is unclear, making it difficult to incorporate this mechanism in climate–carbon-cycle models. It is also unknown why the positive impacts of increasing daily minimum temperatures on productivity are largely confined to arid regions[59] (Fig. 6b). Predicting the net effect of the diurnal non-uniform warming on the terrestrial carbon cycle requires a deeper understanding of diurnal scale processes, and the consideration of specific day and night temperature trends in different regions (Fig. 2).

Carbon cycle uncertainties with non-uniform warming

Trends in climate warming that are non-uniform through space and time have clear consequences for ecosystem carbon cycling. Spring warming will enhance ecosystem carbon uptake at high latitudes (Fig. 5a,b,e) and diminish the magnitude of seasonal temperature change in these regions (Fig. 1b). Summer and autumn warming are more likely to reduce ecosystem carbon uptake in tropical ecosystems (Fig. 5b,c,f) and amplify the magnitude of seasonal temperature change (Fig. 1b). The impact of day and night warming on productivity and vegetation greenness varies between regions (Fig. 6), but the underlying mechanisms remain unclear. Day warming increases carbon uptake in most areas of tundra and boreal forests, but decreases it in most grasslands and deserts (Fig. 6a). Night warming enhances carbon uptake in arid ecosystems such as grassland and desert, but has negative impacts on carbon uptake in other regions (Fig. 6b).

We lack the capability to predict the effects of non-uniform climate warming on terrestrial carbon cycling, in part because most of the existing temperature-manipulation experiments have relied on continuous and uniform warming (Supplementary Table 2 and Fig. 6). We also do not know how to scale results from experimental studies at individual sites up to regional and global levels, so that the findings can be used to evaluate model performance[75,76]. Some biogeochemical models with daily or longer time steps (defined as the interval between one set of solutions and the next)[31,77] are not able to capture the response of the carbon cycle to climate change. The satellite–model mismatch in the response of primary production to a rise in daily minimum temperature (Fig. 6) suggests that experimental studies should be used to benchmark the modelled response of carbon cycling to non-uniform warming. Altogether, it is clear that additional efforts are needed to integrate experiments and models for the in-depth understanding of climate–carbon-cycle feedbacks under non-uniform warming scenarios.

Establishing the impact of non-uniform climate warming on terrestrial carbon cycling is clearly a pressing challenge in the field of carbon cycle research. But non-uniform warming is just one aspect of climate change. Regime shifts in precipitation[78] and disturbances such as wildfires[79], increases in the frequency of extreme temperature events[80], large year-to-year shifts in temperature[81] and shifts in regional climate zones[82] can also be expected as the climate warms. A full understanding of the consequences of climate change for carbon cycling on land will require insight into the impact of all of these changes on ecosystem carbon gain and loss.

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Author contributions

S.W., J.C. and J.X. designed the study. J.X. performed the analyses. J.X., S.W., J.C., S.P. and P.C. drafted the paper. Y.L. contributed to the interpretation of the results and analytical tools. All authors contributed extensively to the revisions of the manuscript.