Seasonal biological carryover dominates northern vegetation growth

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The state of ecosystems is influenced strongly by their past, and describing this carryover effect is important to accurately forecast their future behaviors. However, the strength and persistence of this carryover effect on ecosystem dynamics in comparison to that of simultaneous environmental drivers are still poorly understood. Here, we show that vegetation growth carryover (VGC), defined as the effect of present states of vegetation on subsequent growth, exerts strong positive impacts on seasonal vegetation growth over the Northern Hemisphere. In particular, this VGC of early growing-season vegetation growth is even stronger than past and co-occurring climate on determining peak-to-late season vegetation growth, and is the primary contributor to the recently observed annual greening trend. The effect of seasonal VGC persists into the subsequent year but not further. Current process-based ecosystem models greatly underestimate the VGC effect, and may therefore understate the CO₂ sequestration potential of northern vegetation under future warming.

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Biological cycles include many successional growth periods in which the past and the present are tightly connected. In such temporally connected dynamical systems, transient carryover of the near past is commonly observed for many state variables \(^1\). The carryover effect of biological states has been extensively documented in biomedical research, for example, describing the phenomenon where the effects of medical treatments can carry over from one to another in repeated clinical experiments \(^6\). This biological carryover effect is also widely existent in plant science \(^4\). The life-cycle continuity of plant growth implies that present states of vegetation growth may intrinsically affect subsequent growths, which is a type of biological memory \(^2\), and can be referred to as vegetation-growth carryover (VGC). The VGC effect could potentially control the pattern of seasonal-to-interannual variations of vegetation growth. For example, a tree may maintain a greening signal by cumulatively enhancing carbon uptake \(^*\), resulting in extra storage of photosynthate and more substantial leaves and roots. Such structural change of plants may then boost their resistance to water and heat stress exceeds the tolerance of sustainable tree growth \(^11\). The critical question is thus how strong this VGC effect is, particularly when compared against concurrently changing environmental conditions that also influence the present state of vegetation growth.

Projections of future vegetation and carbon uptake changes, including ecosystem capacity to offset CO\(_2\) emissions, are highly uncertain \(^{12,13}\), primarily due to our limited understanding of the mechanisms that govern vegetation growth dynamics. Surprisingly, while the concept of vegetation carryover effect is not new, and some key analyses searching for evidence of the VGC effect do exist, they are often focused on the short-term carryover \(^{14}\) or limited in their spatial scope \(^{15}\). Over a broad geographical range, it remains unclear how substantial the role of the VGC effect is in contributing to current and future vegetation growth and carbon cycle, particularly in comparison to that of abiotic factors (such as immediate and lagged impacts of climate). Indeed, the regulation of vegetation growth by abiotic factors, particularly climate and associated episodic climate extremes, has been extensively investigated and fairly well understood \(^{16–22}\). It is generally accepted that climate variation is the primary driver of seasonal-to-interannual dynamics of vegetation growth and associated carbon uptake over the Northern Hemisphere (NH) \(^{16–18}\). Importantly, climate change in the early growing season (EGS) may substantially influence vegetation growth of late seasons through, for instance, modulating plant transpiration \(^{19,23–26}\) and snow melting \(^{27,28}\), both leading to changes in soil moisture that can propagate into late seasons \(^{25}\). This climatic legacy effect via complex vegetation-soil-climate interactions has been now included in many state-of-the-art terrestrial biosphere models \(^{29}\). Still, these models produce a wide divergence in the estimates of vegetation growth and carbon uptake \(^{12,13}\), suggesting that some related mechanisms are either missing or incorrectly parameterized.

The interseasonal connections of vegetation growth has received increasing attention in recent years. The legacy effect of EGS vegetation growth on mid-to-late-season growth through transpiration-regulated soil moisture changes \(^{19,23,25,26}\) can be categorized as an exogenous memory effect under the theoretical framework of ecological memory by Ogle et al. \(^2\). Different from the legacy effect of climate anomalies or the exogenous memory of vegetation growth, the VGC effect in this work emphasizes how the carryover of the early vegetation structure may contribute to vegetation growth of the following seasons, or an endogenous memory effect according to the framework of Ogle et al. \(^2\).

In this study, we hypothesize that the VGC has played a critical role in regulating the seasonal-to-interannual trajectory of vegetation growth. To test this hypothesis, we quantify the impact of VGC on NH vegetation growth with a large set of measurements, including satellite, eddy covariance (EC), and tree-ring chronologies, and compare the size of this effect against that of immediate and lagged impacts of climate change (see “Methods”). Our work provides quantitative evidence that peak-to-late season vegetation productivity and greenness are primarily determined by a successful start of the growing season (via the interseasonal VGC effect), rather than by a transient or lagged response to climate. This carryover of seasonal vegetation productivity also contributes to annual vegetation growth across consecutive years.

**Results and discussion**

**Interseasonal VGC dominates peak-to-late season growth.** We first examined the VGC effect at the seasonal scale, using satellite-derived Normalized Difference Vegetation Index (NDVI, see “Methods”) for the 1982–2016 period. We defined the dormancy season (DS) and three periods of the growing season, i.e., EGS, peak growing season (PGS), and late growing season (LGS), based on phenological metrics (see “Methods”). The partial autocorrelation calculated for NDVI time series of two consecutive seasons, after factoring out concurrent and preceding climatic impacts, provides an estimate of the interseasonal VGC effects (see “Methods”). At the hemispheric scale, our analyses show a significant \((p < 0.05)\) control of the NDVI of the preceding season (NDVips) on the interannual variations of seasonal NDVI for all three active growing seasons (Fig. 1a). This VGC effect is also consistently positive across the majority (79%, 89%, and 94% for EGS, PGS, and LGS, respectively) of northern vegetated areas (Supplementary Fig. 1). Although the EGS NDVI is more strongly correlated with EGS temperature, the PGS and LGS NDVIs are most strongly correlated with NDVips, rather than climate drivers (Fig. 1a). This VGC is particularly important for understanding vegetation growth in LGS, when climate is known to have a weak explanatory power \(^{30,31}\).

The primary role of NDVips in driving subsequent PGS and LGS NDVI variations is reaffirmed by conducting partial correlations with detrended anomalies of all variables (Supplementary Fig. 2), implying a robust coupling of seasonal vegetation growth within a specific calendar year. Furthermore, the robustness of the satellite-identified positive VGC effect dominating vegetation growth in PGS and LGS is also verified by examining other satellite-derived vegetation growth proxies, including leaf area index (LAI) and gross primary productivity (GPP) (see “Methods”; results in Supplementary Fig. 3). Meanwhile, we also noticed some difference between GPP- and NDVip-derived LGS-to-EGS VGC effect in some mid-to-high northern latitudes (Supplementary Fig. 4d). Negative LGS-to-EGS VGC effect has been found over eastern U.S., North China, and western and central Russia based on the GPP dataset (Supplementary Fig. 4d), suggesting greater uncertainties in LGS-to-EGS VGC effect than EGS-to-PGS and PGS-to-LGS VGC effects.

In contrast to the consistently strong and positive VGC impact, the strength and direction of climatic factors in determining the interannual variation of seasonal NDVI, including their immediate and lagged impacts \(^{16–20}\), is highly variable between seasons and across regions (Fig. 1a and Supplementary Figs. 5 and 6). At the hemispheric scale, concurrent seasonal temperature is a primary and positive factor controlling the interannual variation of EGS NDVI during the last 35 years (partial correlation, \(r_p = 0.83, p < 0.01\)). The dominance of EGS temperature on EGS vegetation growth is also consistently observed when analyzing other satellite-based vegetation proxies of LAI and GPP (Supplementary Fig. 4). However, temperature has a much weaker impact during PGS \((r_p = 0.42, p < 0.05)\) and LGS \((r_p = 0.12, p > 0.05)\) (Fig. 1a). Although higher concurrent temperature
...growth in EGS across most of the northern vegetated areas (Supplementary Fig. 5a), it has emerged as a limit to PGS and LGS vegetation growth for most of the warm mid-latitudes and some of the high latitudes (Supplementary Fig. 5b, c). Additionally, temperature also has a negative legacy effect on vegetation growth in the subsequent season (Fig. 1a), most significantly for the DS-to-EGS legacy effect ($r_p = -0.42, p < 0.05$). This adverse legacy effect of DS temperature is likely due to the lower chilling accumulation required for leaf unfolding in EGS caused by DS warming. For precipitation, we find very weak and statistically insignificant immediate and lagged impacts on vegetation growth for all the seasons at the hemispheric scale (Fig. 1a). This weak precipitation impact is likely due to a spatial cancelling-out of the positive effects at the water-limited mid-latitudes by the negative effects at high latitudes (more precipitation is often concurrent with increased cloudiness and reduced solar radiation reaching vegetation canopies) (Supplementary Figs. 5d–f and 6d–f).

For each season, we further derived the individual contributions of VGC, as well as the immediate and lagged climatic effects, to the 35-year NDVI trends (see “Methods”). The effects of temperature and precipitation were here combined as a single variable of climatic effects. As expected, the strong observed EGS greening trend ($0.0012 \text{yr}^{-1}, p < 0.05$) is predominately attributed to the concurrent climate change (77%), particularly EGS warming that stimulates earlier phenology, followed by smaller but non-negligible contributions from climate (8%) in the preceding DS and vegetation growth in the preceding LGS (17%) (Fig. 1b). However, for PGS and LGS, about half of the observed greening trends (48% and 54%, respectively) are attributed to greening in the preceding season, and LGS, about half of the observed greening trends (48% and 54%, respectively), and precipitation changes cannot account for the cross-site connections with seasonal GPP data from the global FLUXNET EC network. The short temporal coverage of EC records prevents calculating temporal correlations, we hence analyzed the relationship between the trend of GPP and that of its potential drivers across 50 available flux-tower sites (“Methods”). Consistent with the satellite-based findings, we discovered strong positive cross-site correlations between the trend of GPP and that of its preceding values for all the growing seasons (Pearson correlation, $r = 0.42$, 0.70, and 0.82 for EGS, PGS, and LGS, respectively, $p < 0.01$ in all cases; Fig. 2a). However, temperature and precipitation changes cannot account for the cross-site variation of GPP trends for any season (Supplementary Fig. 8), even though EGS temperature is identified as the primary driver of satellite-based EGS NDVI changes (Fig. 1a). The weak cross-site correlation with climatic variables may be overshadowed by the biome-dependent sensitivity of GPP to climate. To test this, we examined the cross-site relationship between the GPP trend and its climatic sensitivities (“Methods”). We found a significant positive correlation between the EGS GPP trend and...
its sensitivity to temperature ($r = 0.29, p < 0.05$) (Fig. 2b), supporting that EGS warming controls EGS greening patterns. For all the other cases, the insignificant ($p > 0.05$) relationship between the GPP trend and its climatic sensitivity (Fig. 2b, c) supports a weak climatic impact.

In addition to these global datasets, we also used long-term GPP measurements from 11 AmeriFlux EC sites (“Methods”) to characterize temporal relationships between vegetation growth and climate. Results of this analysis again confirm our main findings: EGS temperature is the primary determinant of EGS greening patterns. For all the other cases, the insignificant ($p > 0.05$) relationship between the GPP trend and its climatic sensitivity (Fig. 2b, c) supports a weak climatic impact.

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The persistence of the VGC effect into the subsequent year. In order to examine whether this VGC effect operates at longer time scales of multiple years, we next performed lagged partial auto-correlations with interannual anomalies of satellite-observed NDVI and 2739 standardized tree-ring width (TRW) records (see “Methods”). For a time lag of 1 year, a positive interannual VGC is present across northern lands, with 75.6% of vegetated areas (for NDVI) and 82.9% of the tree-ring samples (for TRW) showing positive lagged correlations (Fig. 4a and Supplementary Fig. 12). This positive interannual VGC indicates that a greener year is often followed by another greener year. The positive VGC is statistically significant ($p < 0.05$) for 18.3% of northern areas based on NDVI, but noting it is significant for 46.4% of the tree-ring samples that cover much longer periods (Fig. 4a). The positive interannual VGC effect is most significant at high latitudes, particularly over northern North America and East Siberia (Supplementary Fig. 12). Interestingly, by further grouping tree species into ring-porous, diffuse-porous and non-porous species (Supplementary Table 1), we found stronger interannual VGC effect for diffuse-porous species (95.0% positive) than for ring-porous (85.3% positive) and non-porous species (81.9% positive) (Fig. 4b). This observation suggests substantial influence of wood phenology on the strength of vegetation growth carryover, and diffuse-porous species whose woody growth is more concentrated in later growing season are more likely to carry transient growth anomalies over to the subsequent year. By contrast, only a few locations (including central Siberia, eastern Europe, and some semi-arid regions) have a negative yet generally insignificant ($p > 0.05$) interannual VGC (Supplementary Fig. 12). If the time lags are extended to 2 years, the positive correlation between current-year NDVI (or TRW) and that of 2 years earlier is significant for 46.4% of the tree-ring samples (for NDVI). If time lags of 3 years are considered, the lagged correlation is found to be close to zero (Fig. 4a). However, for interannual anomalies ($\pm 1$ SD) of vegetation growth that is much less deviated from the multi-year average than severe drought anomalies, the VGC effect can be carried over to the next year but rarely to years after that.

Terrestrial biosphere models underestimate the VGC effect. Process-based terrestrial biosphere models are a useful tool for predicting vegetation growth and examining the associated complex mechanisms$^{29,31}$. We next assessed 16 terrestrial biosphere models participating in the TRENDY intercomparison project (“Methods” and Supplementary Table 2) for their ability to capture the dominant factors contributing to the satellite-observed greenness changes in each season. By comparing modeled GPP (Fig. 5b, of multi-model mean) against satellite-
observed greenness (Fig. 5a), we found that the models correctly identified EGS temperature as the primary factor controlling interannual variations of EGS vegetation activity for most northern areas. In 15 out of the 16 models, areas where EGS temperature is the primary driver of concurrent GPP variations were found to have the largest spatial coverage among all potential driving factors (Fig. 5c). However, the satellite-identified dominance of VGC effects in PGS and LGS vegetation growth for much of the northern lands (42% for PGS and 58% for LGS; Fig. 5d, g and Supplementary Fig. 13b, c) is significantly underestimated by models (19% for both PGS and LGS; Fig. 5e, h and Supplementary Fig. 13e, f). Multi-model averaged results indicate an overwhelming fraction of vegetated land is instead dominated by the immediate climatic effects for both PGS (75%) and LGS (78%). Specifically, 10 out of the 16 models significantly underestimate the proportion of VGC-dominated areas for PGS vegetation greening, and nearly all (15) of the models significantly underestimate the proportion for LGS vegetation growth, despite the strong intermodel discrepancy in the proportion of projected VGC-dominated areas (from 14% in LPX-Bern to 72% in SDGVM for PGS and from 9% in LPJ-wsl to 75% in SDGVM for LGS) (Fig. 5f, i).

With rising atmospheric CO₂ concentrations and anticipated warmer climate, Earth system models that simulate stronger VGC effects tend to project higher carbon uptake potentials over northern ecosystems (Supplementary Fig. 14). To improve estimates of how the global carbon cycle will evolve in the decades ahead, it is critical to diagnose the causes of this underrepresentation of modeled VGC effects. We therefore compared the three models that best identify the areas identified by satellite where VGC dominates vegetation growth versus the three models that least capture it (based on Fig. 5f, i). As expected, we find that the models with the best representation of the VGC effect produce better estimates of PGS and LGS levels of greenness based on EGS growth levels, for all the three major biomes (Supplementary Fig. 15a, c, e). Conversely, for the models that fail to replicate the VGC effect, modeled years with the greenest EGSs do not necessarily imply a greener PGS or LGS, especially for temperate grasslands and forests (Supplementary Fig. 15b, d).

**Conclusions and implications.** In summary, our analyses reveal strong biological carryover effects of vegetation growth and productivity across succeeding seasons and years, providing new insights into how vegetation changes under global warming. The VGC effect represents a key yet often underappreciated pathway through which warmer EGSs and associated earlier plant phenology subsequently enhance plant productivity in mid-to-late growing season, which can further persist into the following year (Fig. 6). Without considering this biological carryover of vegetation growth, some previous studies suggest an overly negative impacts of EGS warming on PGS/LGS vegetation growth, in particular, through triggering earlier transpiration and associated soil moisture deficits. Yet, despite the potential for raised soil moisture deficits, we find the strong VGC effects can override this negative biotic legacy impacts, with greener EGSs ensuring lush PGS vegetation (Fig. 6). Hence, warming in EGS not only augments concurrent vegetation growth and carbon uptake but also has a positive legacy impact on the following PGS.

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**Fig. 4 Observed interannual vegetation growth carryover.** a The histogram shows the frequency distribution of the partial correlations between Normalized Difference Vegetation Index (NDVI), or tree-ring width, of each year and that of the preceding year, after controlling for the climatic variable of both years. Frequency distribution of the partial correlations between tree ring width of each year and that of the preceding year, for ring-porous, diffuse-porous, and non-porous trees (classification details in Supplementary Table 1). Numbers show the percentage of grids (or tree samples) showing statistically significant ($p < 0.05$) negative/positive partial correlations, with the bracketed numbers showing the percentage of all negative/positive correlations. The inset plot of a shows the percentage of grids (or tree samples) showing significantly ($p < 0.05$) positive correlation between present and preceding years’ NDVI (or tree ring width) with lead times ranging from 1 to 3 years. Note that all variables are detrended before performing partial correlation analysis.

| Lead time (years) | Negative: | Positive: |
|-------------------|-----------|-----------|
| 1                 | 1.8 (17.1)% | 46.4 (82.9)% |
| 2                 | 0.8 (24.4)%  | 18.3 (75.6)% |
| 3                 | 0 (14.7)%    | 0 (5%)     |

**Fig. 5 Observed biogeographic differences in vegetation greening.** a The histogram shows the frequency distribution of the partial correlations between tree ring width of each year and that of the preceding year, for ring-porous, diffuse-porous, and non-porous trees (classification details in Supplementary Table 1). Numbers show the percentage of grids (or tree samples) showing statistically significant ($p < 0.05$) negative/positive partial correlations, with the bracketed numbers showing the percentage of all negative/positive correlations. The inset plot of a shows the percentage of grids (or tree samples) showing significantly ($p < 0.05$) positive correlation between present and preceding years’ NDVI (or tree ring width) with lead times ranging from 1 to 3 years. Note that all variables are detrended before performing partial correlation analysis.

| Lead time (years) | Negative: | Positive: |
|-------------------|-----------|-----------|
| 1                 | 0 (14.7)%    | 41.5 (85.3)% |
| 2                 | 0 (5%)       | 54 (95%)   |
| 3                 | 2.2 (18.1)%  | 46.9 (81.9)% |
and LGS vegetation carbon sequestration, ultimately enhancing the annual carbon sink. However, it is important to bear in mind that, while the beneficial VGC effect of EGS vegetation growth can override immediate and time-lagged climatic impact under the present climate, whether this stronger VGC effect will continue with future warmer climate remains an open question (Fig. 6). Processes involved in the lagged vegetation responses to precedent climate, soil, and growth conditions are highly complex and often non-linear\textsuperscript{6,39,40}. For example, summer climate extremes, which are often associated with large-scale climate oscillations and partly contributed by enhanced EGS vegetation growth\textsuperscript{25}, could trigger severe tree mortality and fires that nullify...

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**Fig. 5** Observed versus modeled vegetation growth carryover effects. Spatial patterns show the relative contributions of vegetation growth carryover (VGC) and climatic factors of the present and preceding seasons to the interannual variations of Normalized Difference Vegetation Index (NDVI) or gross primary productivity (GPP). Maps in the left column represent satellite-observed NDVI, and those in the right are the model ensemble-mean GPP for early growing-season (EGS) (a, b), peak growing-season (PGS) (d, e), and late growing-season (LGS) (g, h). Ternary diagrams in c, f, i show the relative fraction of global vegetated areas where the interannual trend of GPP (or NDVI) is dominated by each different driver (corresponding to the maps in each row). Both percentages of the model ensemble-mean (closed blue circles) and the individual models (open symbols) and of satellite observation-based estimates (closed black circles) are shown.

**Fig. 6** Schematic representation of the vegetation growth carryover. The green curves indicate anomalies of vegetation greenness/productivity in response to climatic changes and disturbances, relative to the climatological seasonal cycle (the gray line). Early growing-season (EGS) warming stimulates extra vegetation growth and productivity, and this ecological benefit can persist into peak and late growing-season (PGS and LGS) and even the subsequent year because vegetation growth is largely determined by its prior states (i.e., the vegetation growth carryover, VGC). This greening signal from EGS, however, may be suppressed or even reversed for some locations due to climate extremes or soil moisture deficit legacy from EGS. The symbols $-$ and $+$ in each bracket represent either a negative or positive force respectively imposed on terrestrial vegetation.
Methods

Satellite-based vegetation growth and land-cover maps. Normalized Difference Vegetation Index (NDVI) is commonly used as a proxy for vegetation biomass and photosynthetic activity. Here, NDVI data were obtained from the Global Inventory Monitoring and Modeling Studies (GIMMS) third-generation NDVI product (NDV13g) based on retrievals from sensors on the Advanced Very High Resolution Radiometer (AVHRR)42,43. The GIMMS NDV13g dataset is available at a spatial resolution of 8 × 8 km2 and a biweekly temporal resolution, covering the 1982–2016 period. We composited the biweekly NDVI to monthly values by selecting the highest values.

Considering that NDVI may saturate in densely vegetated areas, we also included two other satellite-based products, LAI and GPP, to independently verify the robustness of NDVI-based findings. Biweekly maps of the global land LAI were derived from the GIMMS AVHRR LAI3g44, with a spatial resolution of 8 × 8 km2 for the period 1982–2016. The monthly gridded GPP maps at 0.5° spatial resolution for 2001–2015 were derived from the remote sensing-based (RS) product of the FLUXCOM database45,46. This dataset was generated with upscaling approaches based on satellite and machine learning models that integrated earth-based carbon fluxes and satellite measurements from Moderate Resolution Imaging Spectroradiometer (MODIS)45,46. The effects of climate and VGC on vegetation changes can vary among ecosystem types. Therefore, we investigated the climatic and VGC impacts separately for the three major vegetation types of temperate grassland, forest (temperate and boreal), and arctic tundra and shrubland. We used the 300-m resolution global land-cover maps for 1992–2016 provided by the European Space Agency’s Climate Change Initiative (ESA-CCI)47 to delineate the three major vegetation types. These maps characterize the global surface using 37 land-cover classes by the International Geosphere-Biosphere Programme (IGBP)48. We grouped the original UNLCCS classes into forest, shrub, and grassland based on the cross-walking table provided by the ESA-CCI land cover product47. We did not consider shrub as a separate group in temperate regions, but assigned this type evenly to grasses and forests. In this study, temperate grassland was defined as water-limited grassland distributed in warm mid-latitude regions, but excluding temperature-limited grassland in pan-Arctic regions and the Tibetan Plateau. The forest type includes evergreen needleleaf forests, evergreen broadleaf forests, deciduous needleleaf forests, deciduous broadleaf forests, and mixed forests. The arctic tundra and shrubland was defined as temperature-limited grassland and shrubland over high latitudes (>50°N). We aggregated the land-cover maps into 0.5° resolution, and calculated the fraction of the above three vegetation types in each 0.5° grid. We only selected grid cells for which the dominant vegetation type occupied >60% of the grid area over the entire period of 1992–2016 (Supplementary Fig. 9) to minimize potential confounding impacts of other vegetation types or land-cover conversions. We also masked northern tundra ecosystems dominated by cropland, as for these locations, the seasonal vegetation growth is primarily controlled by human management practices such as irrigation, fertilization, cropping schedule, and multi-cropping, rather than environmental drivers.

Climatic and soil moisture data. Environmental variables used here include temperature, precipitation, and soil moisture. Monthly time series of temperature and precipitation were obtained from the Climatic Research Unit (CRU) v4.01 dataset48. This gridded dataset, with a spatial resolution of 0.5°, was constructed by interpolation from meteorological stations based on spatial autocorrelation functions48. This climatic product also provides climatic forcing for TRENDY model simulations, ensuring better comparability between observed and modeled responses of ecosystems to climate. Daily root-zone soil moisture estimates with a spatial resolution of 0.25° over 1988–2016 were derived from the Global Land Evaporation Amsterdam Model (GLEAM) v3.2a49. The GLEAM data have fully assimilated microwave observations of precipitation, surface-soil moisture, and vegetation optical depth (VOD)50. GLEAM incorporates VOD as this enables the parameterization of the effects of water stress and climate change on evapotranspiration49. This knowledge of vegetation response in turn allows characterization of interactions between soil moisture and vegetation growth.

EC measurements. We enhanced the reliability of remotely sensed seasonal vegetation–climate interactions by additional analyses using monthly GPP estimates and climatic variables from the FLUXNET2015 and Ameriflux EC measurement. EC-based GPP values used here were estimated from the direct measurement of net ecosystem CO2 exchange by flux towers, combined with knowledge of plant light-response curves50. This FLUXNET2015 database consists of 212 sites that encompass 13 major vegetation types defined according to the classification system of the International Geosphere Biosphere Programme (IGBP). Here, we selected sites that provided at least 7 years of records, and excluded those labeled as cropland or falling into MODIS-based regions dominated by cropland, leading to a total of 50 EC sites for analysis. Since launched in 1996, the Ameriflux observation network provides half-hourly or hourly flux records that allow for temporal correlation analyses. We obtained a subset of 11 Ameriflux sites (CA-T, US-PA, US-ME, US-NE, US-NY, US-OH, US-VA, US-WC, US-Wb) that provide at least 15 years of data, including GPP flux and meteorological variables.

TRM chronologies. We obtained 2739 standardized TRM chronologies from the International Tree-Ring Data Bank (ITRDB)51 V713 dating to August 2017. All selected tree-ring samples are located in the NH (>30°N), and cover at least 25 years of growing season length from 1901–2016. Each chronology is an average of standardized ring width measurements from typically 10 to 30 trees of the same species. We derived the standardized TRM series by detrending the raw TRM measurements based on the “cubic smoothing spline” approach52. This standardization removes low-frequency signals of wood growth associated with increasing tree age and trunk diameter, while still preserving interannual and interdecadal variabilities53. Site-level standard chronologies were generated by averaging tree-level standardized ring indices with a bi-weight robust mean53.

Process-based ecosystem model simulations. We used an ensemble of 16 process-based terrestrial biosphere models participating in the TRENDY (trends in net land-atmosphere carbon exchange) v8 project54 that provide GPP outputs for regions with a growing season length of 3 months or longer. These models were CABLE, CLM4.5, ISAM, JSBACH, JULES, LPJ-GUESS, LPJ-ws, LPX-Bern, ORCHIDEE, ORCHIDEE-MICT, SDGVM, VISIT, VEGAS, OCN, CLASS-CTEM, and DLEM (details in Supplementary Table 2). All these models performed the same set of factorial simulations following a standard experimental protocol55. In particular, we use TRENDY simulation S2 that was forced by varying both atmospheric CO2 and climate. The historical climatic fields were from the CRU-NCEP V8 dataset, which is a merged product of monthly CRU observations and a 6-h NCEP reanalysis. Global atmospheric CO2 concentrations were from a combination of ice-core records and the NOAA monitoring observations.

Quantifying climatic and VGC effects on vegetation growth. We used satellite-derived NDVI and concurrent climatic data to identify covariation between the observed variation of vegetation growing season lengths (EGS, PGS, or LGS). We considered the NDVI of the preceding season, as well as climatic variables (temperature and precipitation) of both the focused season and the preceding season, as driving factors of seasonal NDVI variations. Here we defined preceding-season NDVI as NDVI of the previous season rather than the preceding DS, since vegetation in DS is dormant and the detection of NDVI is hampered by the presence of snow cover (in cold regions). Periods of different seasons were not defined for each grid cell directly by temperature thresholds56 or fixed months across regions (e.g., spring as March–May)57. Instead, we account for actual phenological seasonality using the climatic and vegetation growing season definitions of satellite-derived NDVI for 1982–2016. We derived the dates for the start of the growing season (SOS) and the end of the growing season (EOS) across the NH (>30°N) from the time when the rate of the daily NDVI change interpolated from the original biweekly NDVI time series was highest and lowest, respectively53. Our analysis is based on the 35-year average of SOS and EOS, since we focus on interseasonal connections of active vegetation growth states (greenness or productivity) instead of the shift of phenological events. PGS was defined as the two consecutive months with maximum NDVI values but not earlier than April or later than October. Grid cells with maximum NDVI occurring before April or after October were not considered. For regions with a growing season length of 3 months or less, PGS was defined as the month with the maximum NDVI value. Accordingly, EGS was defined as the period from the month containing the SOS date to the beginning of PGS, and LGS was from the end of PGS to the month of EOS. The remaining months of a year were defined as the DS. Compared to seasonal descriptions based on temperature thresholds or fixed months, these definitions of seasons allow the timing of phenological events are more suitable for analyzing linkages between different stages of vegetation growth in the active growing season. We aggregated monthly

 any positive carryover effect from EGS (Fig. 6). Recent advances in statistical modelling and machine learning39,41 may provide useful tools for a better understanding of such non-linear vegetation responses. We also find poor representation of the VGC effect in dynamic vegetation models, and as this likely influences predictive capacity of future global carbon cycle changes, a major research challenge is to better simulate biological processes related to this carryover effect. Tackling this challenge requires not only using satellite and ground measurements to refine existing parameterizations, but also using leaf-level measurements to understand the physiological mechanisms controlling VGC patterns and to incorporate new process representation in model components. Long-term manipulative field experiments will also be useful to better characterize VGC features under different imposed meteorological regimes and to provide key process parameters for future model improvements.
analyses, SEM allows partitioning the direct and indirect effects that one variable may have on another, and is thus useful for exploring complex influence networks in ecosystems. In this model, the causality between soil moisture and vegetation growth is determined by EC metrics, the sign of their correlation. Positive correlations indicate a dominance of soil moisture impact on vegetation (soil moisture stimulates growth), while negative correlations indicate a dominance of vegetation impact on soil moisture (growth depletes soil moisture). We used the χ² test (and associated p values), the root mean square error of approximation (RMSEA), and an adjusted goodness-of-fit index (AGFI) to evaluate the fit of the established SEM models. The SEM analysis was implemented using the AMOS (version 21.0) software (Amos Development Corporation, Chicago, USA).

Data availability
All observation and model data that support the findings of this study are available as follows. The AVHRR GIMMS NDVIv2 data are available at http://ecocast.arc.nasa.gov/data/pub/gimms/3g/v2/; The AVHRR GIMMS LAIv2 data are available at cl drvew. bu.edu/modismisr/lai3g-fpar3g.html; The FLUXNET2015 EC measurements are available at http://fluxnet.fluxdata.org/2015/12/fluxnet2015-dataset-release/; The AmeriFlux EC measurements are available at https://ameriflux.lbl.gov/data/download data/; The tree-ring width chronologies from the ITDRB V713 data are available at https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring/; the root-zone soil moisture from the GLEAM v3a data are available at https://www.gleam.eu/; model outputs generated by TRENDY v6 ecosystem models are available from Stephen Stich (s.stich@exeter.ac.uk) or Pierre Friedlingstein (p.friedlingstein@exeter.ac.uk) upon request.

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## Author contributions

S.P. and A.C. designed the research; X.L. performed analysis; X.L., S.P. and A.C. wrote the first draft of the manuscript; K.W., X.L., W.B., C.H., J.P., X.H. and R.B.M. commented on the manuscript; and all authors contributed to the interpretation of the results and to the text.

## Competing interests

The authors declare no competing interests.

## Additional information

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