

LETTER • OPEN ACCESS

## The PeatPic project: predicting plot-scale green leaf phenology across peatlands

To cite this article: Scott J Davidson *et al* 2025 *Environ. Res. Lett.* **20** 114002

View the [article online](#) for updates and enhancements.

### You may also like

- [Spatial extrapolation in soil salinity and future land cover using hybrid machine learning and land change modeler: case study in the Mekong Delta and the Red River Delta](#)  
Huu Duy Nguyen, Quang-Hai Truong, Thi Ha Thanh Nguyen *et al.*
- [Satellite data archives reveal positive effects of peatland restoration: albedo and temperature begin to resemble those of intact peatlands](#)  
Iuliia Burdun, Mari Myllymäki, Rebekka R E Artz *et al.*
- [A systematic mapping review of hydrological hazard management in agent-based systems](#)  
Fredrik Schück, Berit Arheimer, Maurizio Mazzoleni *et al.*



The Electrochemical Society  
Advancing solid state & electrochemical science & technology

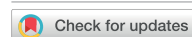


**249th  
ECS Meeting**  
May 24-28, 2026  
Seattle, WA, US  
*Washington State  
Convention Center*

# Spotlight Your Science

**Submission deadline:  
December 5, 2025**

**SUBMIT YOUR ABSTRACT**

ENVIRONMENTAL RESEARCH  
LETTERS

## LETTER

## OPEN ACCESS

RECEIVED  
5 May 2025REVISED  
11 August 2025ACCEPTED FOR PUBLICATION  
12 September 2025PUBLISHED  
10 October 2025

Original content from  
this work may be used  
under the terms of the  
[Creative Commons  
Attribution 4.0 licence](#).

Any further distribution  
of this work must  
maintain attribution to  
the author(s) and the title  
of the work, journal  
citation and DOI.

The PeatPic project: predicting plot-scale green leaf phenology  
across peatlands

Scott J Davidson<sup>1,2,3,34,\*</sup> , Avni Malhotra<sup>4,33,35</sup> , Vincent E J Jassey<sup>5</sup> , Maria Strack<sup>2</sup> , Elena Aitova<sup>6</sup> , Russell Anderson<sup>7,8</sup> , Lindsey J Atkinson<sup>9</sup> , Janna M Barel<sup>5,10</sup> , Melanie Bird<sup>2</sup> , Clarisse Brehier<sup>11</sup>, Gillian Donaldson-Selby<sup>12</sup> , Emma Duley<sup>1</sup> , Joel Eklof<sup>13,14</sup> , Elvira de Eyto<sup>15</sup> , Gustaf Granath<sup>16</sup> , Alanna Grant<sup>17</sup> , Antonia Hartmann<sup>18</sup> , Aleicia Holland<sup>3</sup> , Vytas Huth<sup>19</sup> , Cheristy P Jones<sup>20</sup> , Sung-Ching Lee<sup>21</sup> , Javier Lopatin<sup>22</sup> , Alice M Milner<sup>23</sup> , Mike Peacock<sup>24,25</sup> , Matthias Peichl<sup>18</sup> , Jorge F Perez-Quezada<sup>26,27,28</sup> , Clarice R Perryman<sup>29</sup> , Amy Pickard<sup>17</sup> , Helena Rautakoski<sup>30</sup> , Ewen Silvester<sup>3</sup> , Anna-Maria Virkkala<sup>31,32</sup> and Emma Wegener<sup>2</sup>

- <sup>1</sup> School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, United Kingdom
- <sup>2</sup> Department of Geography and Environmental Management, University of Waterloo, Waterloo, ON, Canada
- <sup>3</sup> Department of Ecological, Plant and Animal Sciences, School of Agriculture, Biomedicine and Environment, La Trobe University, Albury-Wodonga Campus, Victoria, Australia
- <sup>4</sup> Biological Sciences Division, Pacific Northwest National Laboratory, Richland, WA, United States of America
- <sup>5</sup> Université de Toulouse, Toulouse INP, CNRS, IRD, CRBE, Toulouse, France
- <sup>6</sup> Discipline of Geography and The Ryan Institute, University of Galway, Galway, Ireland
- <sup>7</sup> Friends of Leadburn Community Woodland, Leadburn, United Kingdom
- <sup>8</sup> Forest Research, Roslin, Midlothian, United Kingdom
- <sup>9</sup> School of Environmental and Life Sciences, University of Hull, Hull, United Kingdom
- <sup>10</sup> Ecology & Biodiversity, Institute of Environmental Biology, Department of Biology, Faculty of Science, Utrecht University, Utrecht, The Netherlands
- <sup>11</sup> University of Applied Sciences Weihenstephan-Triesdorf, Friesing, Germany
- <sup>12</sup> James Hutton Institute, Aberdeen, United Kingdom
- <sup>13</sup> Civil and Environmental Engineering, University of Washington, Seattle, WA, United States of America
- <sup>14</sup> Department of Environmental Studies and Sciences, University of Puget Sound, Tacoma, WA, United States of America
- <sup>15</sup> Marine Institute, Furnace, Newport, Co., Mayo, Ireland
- <sup>16</sup> Department of Ecology and Genetics, EBC, Uppsala University, Uppsala, Sweden
- <sup>17</sup> UK Centre for Ecology & Hydrology, Edinburgh, Bush Estate, Penicuik, Midlothian, United Kingdom
- <sup>18</sup> Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden
- <sup>19</sup> Peatland Science, Institute of Botany and Landscape Ecology, University of Greifswald, Partner in the Greifswald Mire Centre, Greifswald, Germany
- <sup>20</sup> Department of Earth Sciences and the Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH, United States of America
- <sup>21</sup> Department of Biogeochemical Integration, Max Planck Institute for Biogeochemistry, Jena, Germany
- <sup>22</sup> Faculty of Engineering and Science, University Adolfo Ibáñez, Santiago, Chile
- <sup>23</sup> Department of Geography, Royal Holloway University of London, Egham, United Kingdom
- <sup>24</sup> Department of Geography and Planning, School of Environmental Science, University of Liverpool, Liverpool, United Kingdom
- <sup>25</sup> Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden
- <sup>26</sup> Department of Environmental Sciences and Renewable Natural Resources, University of Chile, Santiago, Chile
- <sup>27</sup> Institute of Ecology and Biodiversity, Barrio Universitario, Concepción, Chile
- <sup>28</sup> Cape Horn International Center, Punta Arenas, Chile
- <sup>29</sup> Department of Earth System Science, Stanford University, Stanford, CA, United States of America
- <sup>30</sup> Finnish Meteorological Institute, Helsinki, Finland
- <sup>31</sup> Woodwell Climate Research Center, Falmouth, MA, United States of America
- <sup>32</sup> Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland
- <sup>33</sup> Department of Geography, University of Zurich, Zurich, Switzerland
- <sup>34</sup> Now at: Département des sciences biologiques, Université du Québec à Montréal, Montréal, QC, Canada.
- <sup>35</sup> Joint first author.

\* Author to whom any correspondence should be addressed.

E-mail: [sj davidson989@gmail.com](mailto:sj davidson989@gmail.com)

**Keywords:** peatlands, green leaf phenology, community science, energy balance, environmental change, low cost monitoring

Supplementary material for this article is available [online](#)

**Abstract**

Peatlands store approximately one-third of the world's soil carbon (C), but their functioning is highly variable at fine spatial scales due to differences in vegetation cover and environmental

conditions such as water table depth. This fine-scale heterogeneity plays a key role in carbon dynamics yet capturing it—particularly in relation to green leaf phenology (GLP)—is challenging with traditional remote sensing methods. To address this, we developed a smartphone-based methodology and community-science project called the PeatPic Project. We gathered over 3700 photographs from 27 sites across 10 countries in 2021 and 2022, representing different peatland types (bog, fen, and swamp), at 1–2 week intervals. We calculated GLP metrics, such as the data of the start of the season and end of the season, based on the red-blue-green bands from these photographs. We found that GLP metrics varied significantly across peatland types and dominant vegetation communities. Notably, peak greenness at bog sites occurring approximately 10 days later in the year compared to fen sites. Furthermore, variables relation to peatland/vegetation type and energy balance were key predictors of peatland GLP. The PeatPic Project's readily available methodology offers low-cost opportunities for further research into peatland phenology, enabling the calculation of additional phenological indices and integration with other data types. By refining our understanding of peatland GLP, we can improve predictive C modelling and better assess the impacts of future changes on these important ecosystems.

## 1. Introduction

Peatlands are a type of wetland ecosystem with a thick layer of partially decomposed organic matter. They cover approximately 400 million hectares (~3%) of the world's surface but store disproportionately large amount of the world's soil carbon (C)—estimated at ~600 Gt of C, or 21% of the total global soil C stock (Page *et al* 2011, Yu 2012, Scharlemann *et al* 2014). Their ability to store such large amounts of C means that peatlands have the potential to significantly influence the climate-C cycle feedback (Moore *et al* 1998), act as a nature-based solution to climate change (Strack *et al* 2022, Girkin and Davidson 2024), and influence global C budgets (e.g. Saunois *et al* 2025). To understand peatland roles in local and global C cycling, there has been increased focus on investigating peatland functioning, particularly in relation to interactions between hydrological conditions and C storage (van Bellen and Larivière 2020). However, less attention has been directed to understanding how peatland vegetation communities' function with regards to green leaf phenology (GLP: the phenology of leaf traits, e.g. timing of leaf out, timing of peak greenness and leaf fall) which is an important driver of terrestrial C cycling (Hufkens *et al* 2012).

Changes in temperature and precipitation patterns are altering phenological events in peatlands, potentially affecting their C sequestration capacity (Koebsch *et al* 2020, Davidson *et al* 2021, Köster *et al* 2023, Simpson *et al* 2025). For example, increasing global air temperatures are leading to substantial changes in the timing and duration of ecosystem processes, including plant green-up in the spring and senescence in the autumn (Schädel *et al* 2023), and an overall lengthening of the growing season in many regions (Richardson *et al* 2018, Collins *et al* 2021). However, these investigations

typically focus on ecosystem-scale phenology, where trends in tree-dominated systems may overshadow the dynamics of low-statured understory species (e.g. mosses, shrubs, and graminoids), which dominate peatland productivity in many northern sites. While small statured, these plants can often dominate net primary productivity budgets in peatlands (e.g. Griffiths *et al* 2017). Thus, the GLP of understory plants and its variation across peatlands remains elusive.

Changes in GLP can have significant impacts on net annual C uptake (Hanson *et al* 2020, Koebsch *et al* 2020, Simpson *et al* 2025). Early leaf-out and extended growing seasons may increase C uptake but also result in higher C release during dry periods (Hanson *et al* 2020). Moss-dominated peatlands, such as bogs, generally green up more slowly than graminoid- and shrub-dominated peatlands (e.g. fens), resulting in lower photosynthetic activity earlier in the growing season and impacting C cycling rates through faster C turnover (Blodau 2002, Peacock *et al* 2019). Slow-growing *Sphagnum* mosses can lengthen the growing season in peatlands, extending C sequestration further into the autumn period (Kivimäki *et al* 2008). Different vascular plant species can also be physiologically active at various times of the year, with knock-on effects on C source/sink behaviour (Ström *et al* 2005). The changes in growing season length have also been linked to peat accumulation rates (Gallego-Sala *et al* 2018), suggesting that understanding how plant communities green-up and growing season lengths vary in space and time (and how they are changing in response to climate change) is critical to monitoring long-term peatland C storage (Charman *et al* 2013). Disturbance impacts on peatland vegetation can also alter greenness trajectories, through both changes in the greenness timing of the vegetation present, as well as shifts within the community that can lead to

different greenness characteristics compared to the previous undisturbed community (Davidson *et al* 2021). Thus, the impacts of global change processes on peatland phenology are highly uncertain but likely to be dependent on peatland type, climate, disturbance regime, and other factors.

Digital red–green–blue (RGB) photography is a non-destructive method that can be used to measure and understand plant GLP (Crimmins and Crimmins 2008). Photographs provide visual evidence and detailed records of phenological events in an easily accessible, standardisable, and low-cost manner. They allow for the verification and calibration of observational data and improve accuracy (Barve *et al* 2020) including within prediction and estimation of plot-scale C fluxes (Gutekunst *et al* 2019, Davidson *et al* 2021). There have been ecosystem scale studies looking at peatland vegetation GLP (Peichl *et al* 2015, Koebsch *et al* 2020) using high temporal resolution image archives and studies synthesizing data from networks such as Phenocam (Wingate *et al* 2015, Richardson *et al* 2018) but there are very few plot-scale studies looking at peatland vegetation GLP (Peichl *et al* 2018, Davidson *et al* 2021, Garisoain *et al* 2023). Peatlands are inherently heterogeneous, including a variety of peatland microforms and vegetation communities, associated sub-metre changes in C flux (Riquelme Del Río *et al* 2024), that vary in their response to changing water table and temperature regimes (Strack and Waddington 2007, Munir *et al* 2015). Thus, understanding small-scale ( $\leq 1 \text{ m}^2$ ) resolution of peatland GLP is key to monitoring and predicting peatland functional changes.

Therefore, there is a need for a comprehensive global network of datasets to understand the spatial and temporal variations in peatland GLP at the square-metre scale, to provide a baseline for long-term monitoring to track global change effects. Advances in smartphone technology and online platforms have facilitated the widespread collection and sharing of phenological data through photographs (Hufkens *et al* 2019, Barve *et al* 2020, Tonnang *et al* 2020, Liu *et al* 2022). This method thus provides a promising avenue for peatland GLP research, and one particularly well suited to both community science due to the readily available nature of smartphones (Klinger *et al* 2023) and advances in image processing driven by machine learning algorithms (Fang *et al* 2019, Reichstein *et al* 2019).

Here, we use a standardised smartphone photography method and a community science approach (the PeatPic project) to investigate how peatland greenness trajectories, specifically, day of year at peak greenness, varies across different peatland types. Additionally, we test for site characteristics and environmental factors as predictors of GLP.

We hypothesise that (1) graminoid- and shrub-dominated systems peak in greenness earlier than moss dominated systems, (2) peak greenness will be

earlier in warm climate peatlands compared to cool climate and (3) peatlands at lower latitudes are expected to reach peak greenness earlier than peatlands at higher latitudes.

## 2. Methods

### 2.1. Community photographs

During 2021 and 2022, we recruited project participants via email, social media, and word of mouth amongst the peatland research community. Participants collected plot-scale ( $0.036\text{--}1 \text{ m}^2$ ) photographs of the dominant vegetation communities at their peatland research sites (figure 1) using the standardised PeatPic protocol developed by the project lead (see supplementary information for details).

All sites had between 4–12 plots. Plots were either permanent locations for monitoring vegetation or measuring C fluxes (e.g. collars), or were temporarily marked using quadrats, flags or other markers (examples for each site shown in figure S1). Photographs were collected on a weekly to bi-weekly basis across most sites, dependent on remoteness and logistics, and at all sites photography began before the growing season and continued into the autumn senescence period where logistically possible. Participants were required to have the image acquisition mode set to auto white balance and autofocus, photograph under as clear or overcast sky conditions as possible and to avoid including any shadows in the photo where possible. Photographs were consistently taken from a nadir angle (directly overhead), approximately 1 m above the ground-layer canopy. While different camera/phone sensors were used across sites, for a given site, only one phone or camera type was used.

Alongside the photographs, participants were asked to provide information on the peatland type (bog, fen or swamp), the dominant vegetation community (*Sphagnum*-, feather moss-, graminoid- or shrub-dominated), the microform type (hummock, lawn or hollow), whether the site had tree cover (at site level), whether it was underlain by permafrost (at plot level), and whether there was any evidence of disturbance impact (at plot level).

### 2.2. RGB photography analysis

We used the R package *Phenopix* version 2.4.4 (Filippa *et al* 2016) to calculate the greenness index:

$$\text{Greenness index} = G_{\text{DN}}/R_{\text{DN}} + G_{\text{DN}} + B_{\text{DN}} \quad (1)$$

where the  $R_{\text{DN}}$ ,  $G_{\text{DN}}$  and  $B_{\text{DN}}$  are the average red, green and blue digital numbers respectively. This index was chosen as it is more robust than other indices with regard to scene illumination and shadows (Sonnentag *et al* 2012, Davidson *et al* 2021). Any photos that included snow cover or standing water were omitted from the analysis (approximately 0.2% of the total number of submitted photographs).



We used the R package's *DrawROI* function to hand-identify and delineate a Region-Of-Interest of the dominated vegetation community within the designated plot in each photograph. We then used its *ExtractVIs* function to calculate the index on a per-pixel basis (Toomey *et al* 2015). To compare the seasonal trajectories of the greenness indices between the different peatland types and four vegetation community groups, we fitted a Gaussian model to our measured greenness values by day of the year (DOY; Davidson *et al* 2021). We used the following model to fit data at each unique plot for each year (hereafter, plot-year):

$$\text{Modelled greenness index} = a \times e^{-0.5 \left[ \text{DOY} - \frac{b}{c} \right]^2} \quad (2)$$

where  $a$ ,  $b$  and  $c$  are parameters describing the seasonal trajectory of the greenness index; the peak value ( $a$ ), DOY at peak greenness, ( $b$ ) and the growth rate of the curve ( $c$ ). The parameters allowed us to compare the peak, timing of peak, and progression of GLP across all plots. We focus primarily on the DOY at peak greenness as a descriptor of changes to GLP patterns because sites varied in their specific phone or camera sensor and their greenness values would not be comparable. However, the trajectory of greenness within a site and day of peak value are comparable. For calculating the day of peak greenness, we only used model outputs from equation (2) when  $p$ -value  $< 0.05$ . Out of our total 319 plot-years where we fit the equation (2) model, we had to remove 96 unique plot-years because their model fit  $p$ -value was  $> 0.05$ . Note that to standardise comparisons of southern and northern hemisphere growing seasons, we adjusted the southern hemisphere DOYs by adding 182.5 to any DOY less than 182.5 and by subtracting 182.5 from any DOY greater than 182.5. This allowed for an alignment of the growing season trajectories in both the hemispheres that was necessary for fitting equation (2) to the data.

### 2.3. Predictor data

For predictor data, we used a range of site-reported peatland characteristics and climate reanalysis data from ERA5 (Muñoz Sabater 2019; Download date 18 February 2025). The resolution of the ERA5 data is  $0.25^\circ \times 0.25^\circ$ . We downloaded monthly averaged data (from hourly data) for the years of our photographs (2021 and 2022) for the entire globe and extracted the data for the pixel in which our sites occurred using the *terra* R package (Hijmans 2024). We extracted variables related to our hypotheses (table 1), namely, snow depth, snow albedo, soil and air temperature, incoming solar radiation, surface sensible and latent heat flux, soil moisture, and precipitation. We then averaged all the months

within 2021 or 2022 to obtain an annual average value for each site and year. The only exception was precipitation, which we summed instead of averaged. Note that our precipitation metric is monthly averaged precipitation (based on what the ERA5 product provides) summed annually for the measurement year (2021 or 2022).

### 2.4. Data analyses

All analyses were performed using R version 4.4.2 (R Core Team 2024). We conducted Kruskal–Wallis tests to examine differences between categories, for example, to compare mean DOY at peak greenness values across our three peatland types and vegetation communities. This was followed by pairwise comparisons using a Steel–Dwass post-hoc test to determine significant differences between individual peatland types and vegetation communities. Statistical significance was set at  $p < 0.05$  for all tests.

We implemented Generalised Additive Mixed Models (GAMMs) in R using the *mgcv* package (Wood 2011) to determine the best predictors of peak greenness. We selected GAMM because it accommodates non-linear relationships between predictors and response variables, while also allowing for random effects to account for hierarchical structure and repeated measurements in the data. To minimise overfitting and multicollinearity, we first reduced the full set of environmental covariates (see table 1) by selecting the representative and least collinear variables. We applied a hierarchical clustering approach using the *ClustOfVar* package (Chavent *et al* 2012), which grouped variables into four main clusters based on shared variance (figure S2). To explore model performance across combinations of predictors, we ran 1000 GAMM iterations. In each iteration, we randomly selected one variable from each of the four clusters to include fixed effects, while treating year and camera type as random intercepts to account for temporal and equipment variability. This approach allowed us to address potential issues with multicollinearity, repeated measures, and overparameterization. Each model was trained on 70% of the data (training set) and evaluated on the remaining 30% (test set) of the data to test model predictive performance. We then quantified the predictive performance of each model iteration by computing the coefficient of determination ( $R^2$ ) from predicted versus observed greenness peak values in the test set. Finally, we selected the best-performing GAMM across the 1000 iterations (highest test-set  $R^2$ ) and used its four selected covariates to fit a final GAMM to the entire dataset. Our 1,000 GAMM iterations had relatively good predictive strength, with a mean cross-validation of  $R^2 = 0.18 \pm 0.13$ . Finally, we used the function *gam.hp* (Lai *et al* 2024) to assess the partition of variance explained by each predictor in our best GAMM model.

**Table 1.** Predictor variables included in the Generalised Mixed Effects Additive Models (GAMMs).

| Name                          | Description                                                           | Units                                                          | Source                    | Rationale for using as predictor                                                                                                                    |
|-------------------------------|-----------------------------------------------------------------------|----------------------------------------------------------------|---------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------|
| Latitude                      | Geographic coordinate specifying the north-south position of the site | Degrees (°)                                                    | Site PI reported          | Determines climatic zone and seasonal patterns, affecting the timing of peak vegetation greenness.                                                  |
| Permafrost presence           | Indicates whether permafrost is present at the site                   | Binary (Y/N)                                                   | Site PI reported          | Permafrost affects soil temperature and moisture regimes, influencing plant root systems and the timing of peak vegetation greenness.               |
| Disturbance                   | Indicates whether disturbance is present at the site                  | Binary (Y/N)                                                   | Site PI reported          | Influences a variety of plant growth factors, including phenology                                                                                   |
| Tree cover                    | Indicate whether peatland had a dominant cover of trees or was open   | Binary (Y/N)                                                   | Site PI reported          | Influences understory plant community characteristics                                                                                               |
| Peatland type                 | Indicates what type of peatland the plot was in                       | Bog, fen or swamp                                              | Site PI reported          | Linked to site hydrology and nutrient status, which influence plant phenology                                                                       |
| Dominant vegetation type      | Indicates the dominant vegetation type in the plot                    | Shrub, <i>Sphagnum</i> , feather moss or graminoid dominated   | Site PI reported          | Plant taxonomic groups have varying phenological traits                                                                                             |
| Microform                     | Indicates where plot was located on the landscape                     | Hummock, hollow or lawn                                        | Site PI reported          | Influences a variety of plant growth factors, including phenology                                                                                   |
| Mean annual air temperature   | Annual average air temperature at the site                            | Degrees Celsius (°C)                                           | Climate reanalysis (ERA5) | Influences the length of the growing season and the timing of vegetation development, affecting when peak greenness is achieved.                    |
| Mean annual soil temperature  | Annual average soil temperature at the site                           | Degrees Celsius (°C)                                           | Climate reanalysis (ERA5) | Affects root growth, nutrient uptake, and soil microbial activity, which are critical for plant health and the timing of peak vegetation greenness. |
| Annual precipitation          | Total annual rainfall received at the site                            | Millimetres (mm)                                               | Climate reanalysis (ERA5) | Determines soil moisture levels, influencing plant growth cycles and the timing of peak greenness.                                                  |
| Volumetric soil water content | Water content in the soil within the 0–7 cm layer                     | Cubic metres per cubic metre (m <sup>3</sup> /m <sup>3</sup> ) | Climate reanalysis (ERA5) | Impacts plant moisture and nutrient availability, affecting the timing of peak vegetation health.                                                   |

(Continued.)

Table 1. (Continued.)

|                             |                                                                       |                                               |                           |                                                                                                                                                           |
|-----------------------------|-----------------------------------------------------------------------|-----------------------------------------------|---------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------|
| Snow Albedo                 | Reflectivity of snow cover at the site                                | Dimensionless (0–1)                           | Climate reanalysis (ERA5) | Influences soil temperature and moisture by affecting the amount of solar radiation absorbed, thereby impacting the start and peak of the growing season. |
| Snow depth                  | Thickness of snow cover at the site                                   | Metres (m)                                    | Climate reanalysis (ERA5) | Affects the duration of snow cover, which can delay or advance the onset of the growing season and influence the timing of peak greenness.                |
| Surface net solar radiation | Net solar energy received at the ground or water surface              | Joules per square metre ( $\text{J m}^{-2}$ ) | Climate reanalysis (ERA5) | Determines the energy available for photosynthesis, influencing plant growth rate and the timing of peak vegetation.                                      |
| Surface latent heat flux    | Energy transfer associated with phase changes of water at the surface | Joules per square metre ( $\text{J m}^{-2}$ ) | Climate reanalysis (ERA5) | Influences soil moisture and temperature regulation, affecting plant growth cycles and peak greenness timing.                                             |
| Surface sensible heat flux  | Energy transfer related to temperature changes at the surface         | Joules per square metre ( $\text{J m}^{-2}$ ) | Climate reanalysis (ERA5) | Affects microclimatic conditions, influencing plant metabolism and the timing of peak vegetation greenness.                                               |

### 3. Results

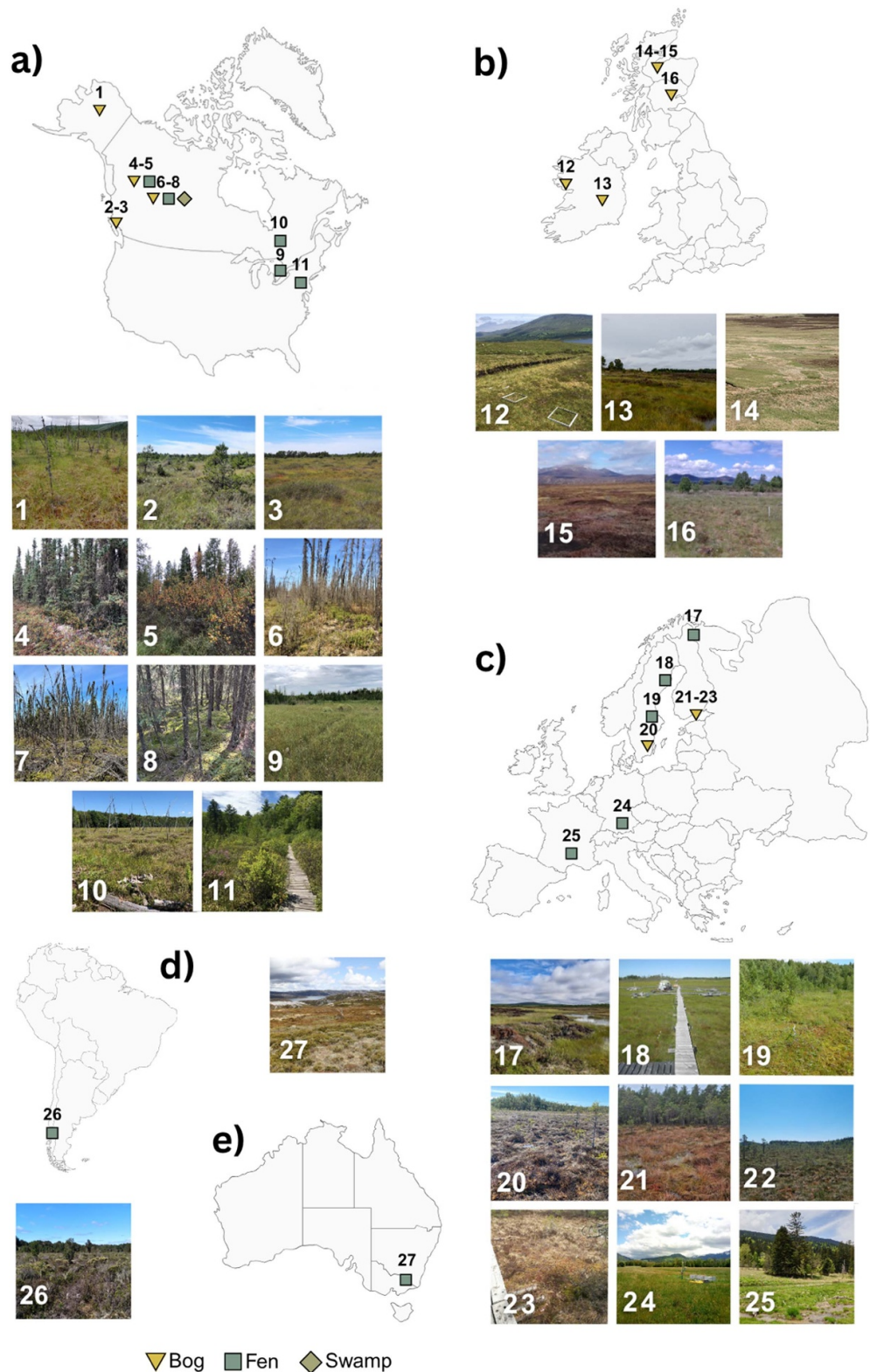
#### 3.1. Description of collected data

In total, over 3700 photographs (2433 in 2021 and 1306 in 2022) were contributed to this project from participants across 164 unique plots distributed among 27 different sites in 10 different countries (figure 1/table S1). Most photographs were collected from bogs (11 open and 3 with trees) and fens (8 open and 4 with trees), with one swamp site (figure S3). Four sites had photographs for both 2021 and 2022 (Bonanza Creek, Cloncrow, Degerö and Senda Darwin). In our dataset, plots were distributed across various vegetation types, microforms, permafrost presence, and tree cover. The majority of data come from graminoid-dominated (33%), shrub-dominated (18%), and sphagnum-dominated (17%) plots. Plots with permafrost present comprise 23% of the data, while treed plots comprise 6% of the data. Regarding microforms, hummocks account for 24% of the data, lawns for 18%, hollows for 11%, while the rest are not specified. Disturbances included historical or modern, e.g. drainage, grazing, oil and gas exploration activities and wildfire. Individual plot

greenness values per site are shown in figure 2 and the mean  $\pm$  SE greenness values for plots across all 27 sites, averaged by day of year, is shown in figure 3. The remaining results focus on our key phenology metric, DOY at peak greenness, that we calculated for each unique plot-year (Methods in section 2.2).

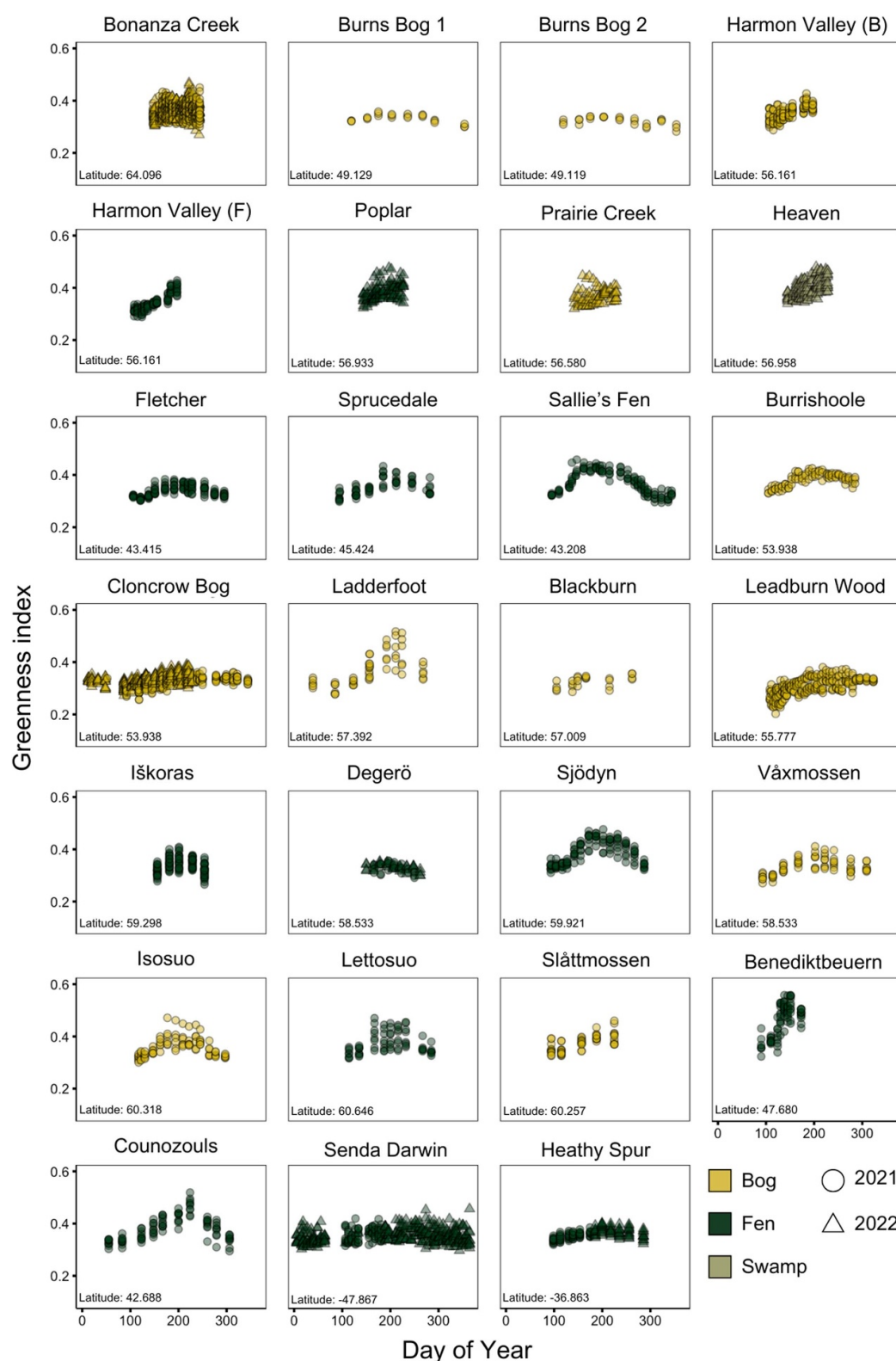
#### 3.2. Variability in GLP

Day of year at peak greenness was significantly different between peatland types (figure 4(A); Chi-square = 34.2;  $p < 0.0001$ ), indicating bog and fen are phenologically significantly different ( $Z = -5.07$ ,  $p < 0.0001$ ). Bog sites had a wider range, with peak greenness occurring a median of 10 d later in the year compared to fen sites. Note that the swamp greenness data were only from one site (Davidson *et al* 2024). Peak greenness also varied among vegetation types (figure 4(B); Chi square = 10.91;  $p = 0.012$ ) with *Sphagnum*- and graminoid-dominated plots showing significant differences ( $Z = -3.16$ ,  $p = 0.0016$ ). Contrary to our hypothesis, graminoid-dominated plots peaked in leaf greenness approximately one week later than *Sphagnum*-dominated ones.



**Figure 1.** Location and photographs of study sites: 1) Bonanza Creek (\*), 2) Burns Bog 1 (\*), 3) Burns Bog 2 (\*), 4) Harmon Valley (\*), 5) Harmon Valley (\*\*), 6) Poplar (\*\*), 7) Prairie Creek (\*), 8) Heaven (\*\*\*), 9) Fletcher (\*\*), 10) Sprucedale (\*\*), 11) Sallie's Fen (\*\*), 12) Burrishoole (\*), 13) Cloncrow (\*), 14) Ladderfoot (\*), 15) Blackburn (\*), 16) Leadburn Wood (\*), 17) Iskoras (\*\*), 18) Degerö (\*\*), 19) Sjödyn (\*\*), 20) Våxmossen (\*), 21) Isosuo (\*), 22) Tervalamminsuo (\*\*), 23) Slåtmossen (\*\*), 24) Benediktbeuern (\*\*), 25) Counozouls (\*\*), 26) Senda Darwin (\*\*) and 27) Heathy Spur (\*\*). \* Indicates bog, \*\* indicates fen and \*\*\* indicates swamp. Note where site names are duplicated (i.e. Burns Bog, Harmon Valley), these represent two distinct sub-sites with different conditions (e.g. different vegetation communities, different experimental manipulations, different disturbance histories). All photographs provided by co-authors.





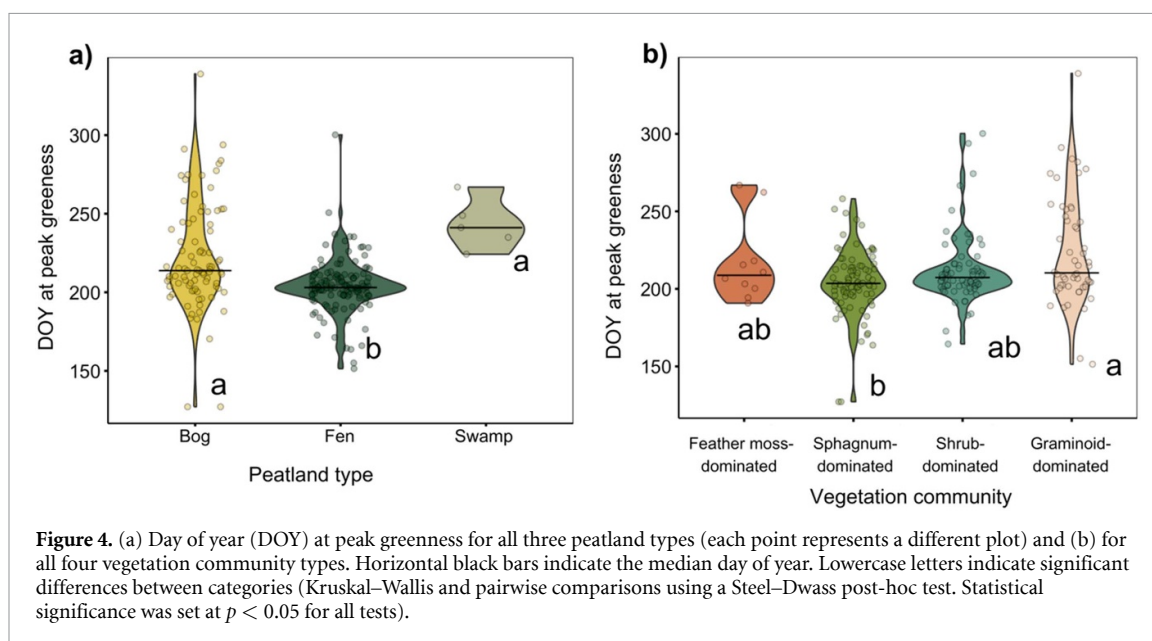
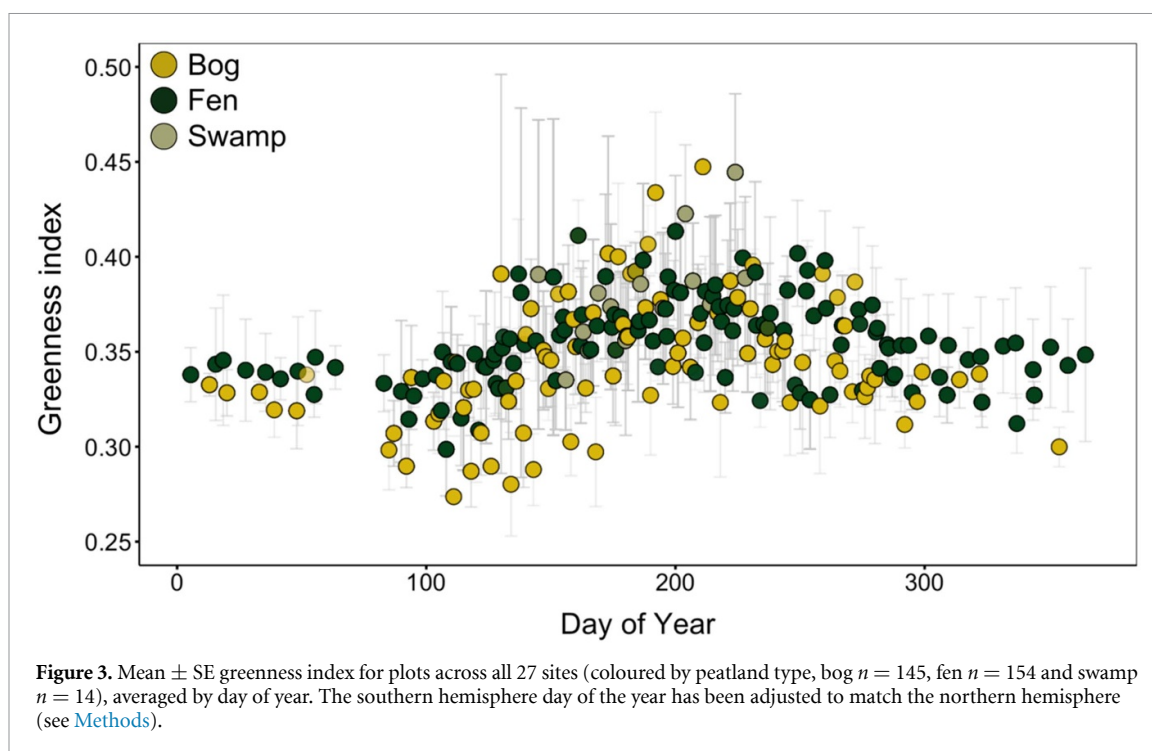
**Figure 2.** Raw greenness index values for all 27 sites across peatland types. Each point represents an individual plot. Day of year adjusted for both southern hemisphere sites (Senda Darwin and Heathy Spur). Circles represent data collected in 2021 and triangles represent data collected in 2022. Four sites collected photographs for both years of the study (Bonanza Creek, Cloncrow Bog, Degerö and Senda Darwin). Note that our Gaussian fits on these data were done on the unique plot-level and not on site-level (see equation (2) in methods).

### 3.3. Predictors of GLP

The GAMM had a predictive strength of  $R^2 = 0.40$  and a deviance explained at 48%. The dominant site characteristics-related predictors of DOY

at peak greenness across our sites were vegetation (16% of total deviance explained) and peatland type (21% of total deviance explained) (figures 4 and 5).

Furthermore, surface net solar radiation (46% of total



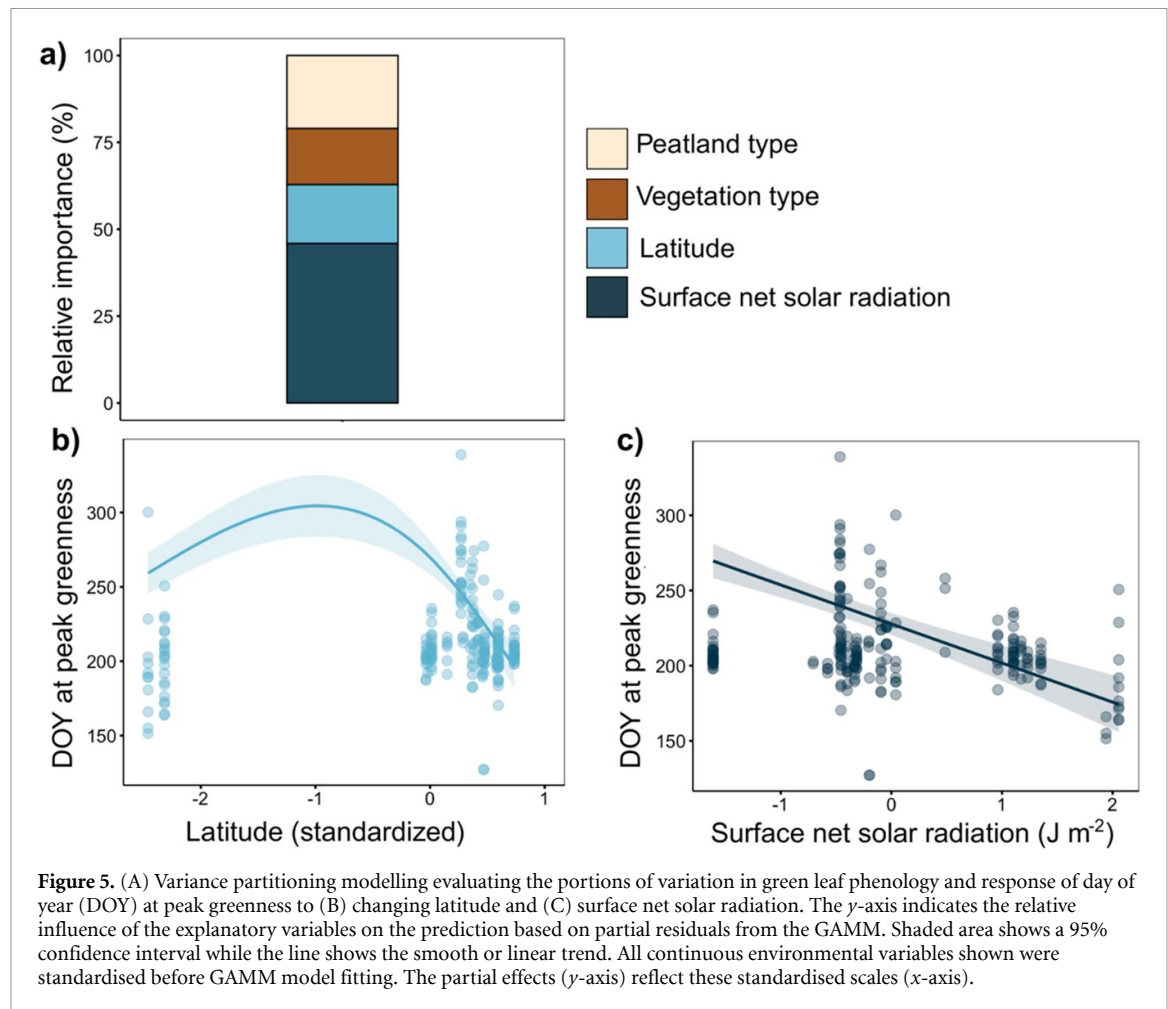
deviance explained) and latitude (17% of total deviance explained) were the most important factors driving GLP across peatlands (figures 5(A)–(C)). As per our hypothesis that peak greenness will be earlier in warm sites compared to cool sites, we found that DOY at peak greenness strongly decreased with increasing surface net solar radiation (figure 5(C)). Similarly, we had expected that DOY at peak greenness would increase going from equator to poles, but this trend was nonlinear, and our results did not support our hypothesis (figure 5(B)), while noting the difference in site distribution along latitude.

## 4. Discussion

Here, we investigated climatic, environmental and vegetation controls on peatland plant community GLP using photographs collected via a community science approach.

### 4.1. Drivers of peatland GLP

Overall, our model explained 48% of variation in peak greenness, indicating that peatland type, vegetation type, latitude and surface solar net radiation are the strongest predictors of DOY at peak greenness.



The variation in DOY at peak greenness was larger in bogs than in fens (figure 4(A)), likely linked to the dominant plant species present. Linked to the strong control of peatland type on GLP, differences in vegetation composition across latitudes also influence GLP. The dominant species in the bog sites in this study, (*Sphagnum* mosses—figure S3), often have slower growth rates and delayed phenological phases, such as leaf emergence and senescence (Garisoain *et al* 2023), resulting from lower nutrient availability (Aerts *et al* 1992). Bog species are adapted to these nutrient poor-conditions and exhibit conservative growth strategies (Laine *et al* 2021), including prolonged periods of leaf retention while having reduced rates of photosynthesis (Huth *et al* 2021), meaning they may stay ‘greener’ or more productive for longer than other peatland types. However, our bog or fen sites were not strictly *Sphagnum* or graminoid dominated as we had expected. Instead, both site types had a mix of different dominant vegetation which may explain this variability (figure S3). Additionally, *Sphagnum* communities may not appear ‘green’ when productive due to either species present or location on landscape (hummock vs. hollow for example) (Letendre *et al* 2008). Contrary to our hypothesis, we observed that *Sphagnum*-dominated plots green up earlier than

graminoid-dominated plots. This could be in part due to the range of climates that the *Sphagnum*-dominated plots spanned, alongside the moss already being green when the snow disappears in comparison to vascular plants that need more time to develop their green biomass.

The typically higher pH and nutrient availability of fens means they support not only a wider diversity in plant species but are primarily dominated by species that favour more rapid growth characteristics i.e. sedges and non-ericaceous shrubs such as *Salix* spp., with different phenological timing. These species often display earlier leaf-out in spring compared to more moss-dominated peatlands (Leppälä *et al* 2008) and faster cycles of growth, senescence, and productivity (Davidson *et al* 2021). Species-specific phenological responses to changing environmental conditions and photoperiods may also vary between peatland types (Peichl *et al* 2018). For example, sedge-dominated fens may exhibit greater sensitivity to air/soil temperature fluctuations and extensions to the growing season, promoting earlier green up (Thayamkottu *et al* 2024).

Although disturbances such as permafrost thaw or tree cover were not found to be significant controls on plot-scale GLP in this study (likely due

to limited replication of permafrost versus non-permafrost peatland or treed versus non-treed peatland sites), these variables could still impact peatland GLP. For example, permafrost thaw could substantially alter peatland GLP by modifying hydrological conditions, soil thermal regimes, and nutrient availability (Keuper *et al* 2012), thereby affecting plant growth timing and duration. As the permafrost degrades, increased active layer thickness and altered water tables may favour species with different phenological strategies, reshaping community-level GLP patterns. Additionally, vegetation structure, particularly tree cover, could also play a critical role in mediating GLP. Davidson *et al* (2021) demonstrated that the removal of tree cover in boreal peatlands following oil and gas exploration disturbances led to a reorganization of the entire vegetation community, rather than a direct alteration of phenology alone, suggesting that GLP responses are often emergent properties of broader community shifts rather than isolated trait-level changes.

As per our hypothesis, warmer sites greened earlier than cool sites, as indicated by surface net solar radiation having a strong influence on DOY of peak greenness. Surface net solar radiation determines the energy available for photosynthesis and thermal regulation, thereby influencing the onset, intensity, and duration of peak peatland vegetative activity (Leonard *et al* 2021, Gu *et al* 2023). Earlier peak greenness often coincides with increased springtime radiation inputs, enhancing photosynthetic efficiency and promoting early canopy development (Ren *et al* 2024). Variability in the DOY of peak greenness at our sites will affect plant productivity and community dynamics, especially in peatlands across northern latitudes, where vegetation is especially sensitive to microclimatic conditions and water availability (Walther *et al* 2018). Shifts in solar radiation regimes due to climate change could therefore alter the phenological trajectory and ecological functioning of peatland systems over time (Antala *et al* 2022).

Our hypothesis that DOY at peak greenness would be later going from equator to poles was not supported. Our results indicate that DOY at peak greenness was earlier in the northern peatland sites (Alaska, northern Canada, Norway and Finland) compared to mid-latitude sites such as the UK or southern Sweden. Alongside the controls on vegetation types present in these peatlands, latitude can also play a critical role through its influence on photoperiod, temperature regimes, and growing season length (Koebsch *et al* 2020). At higher latitudes, extreme seasonal variation in day length exerts a strong control on phenological events (Collins *et al* 2021), with long photoperiods in summer promoting rapid canopy development and short autumn days triggering earlier senescence (Estiarte and Peñuelas 2014). In these regions, temperature constraints often

delay spring green-up due to prolonged snow cover and cooler soil temperatures, while early frosts can prompt premature leaf senescence, leading to a compressed growing season (Bigler and Bugmann 2018).

In contrast, the lower-latitude sites may experience milder climates with longer and more stable growing seasons (Hudson *et al* 2022). These conditions will allow for earlier leaf emergence and extended periods of vegetation greenness, potentially supporting multiple growth peaks depending on hydrological conditions as found in forest ecosystems by Denham *et al* (2023). At the plot scale, local microtopographic variation (e.g. hummocks versus hollows) can modulate these latitudinal effects by altering soil temperature, water table depth, and light availability (van der Molen *et al* 1994, Villa *et al* 2019), leading to spatial heterogeneity in phenological patterns even within a single site.

#### 4.2. A low-cost method and peatland GLP database using smartphone photography

Using a standardised, community science approach, we collected over 3,700 photographs of peatland vegetation at the plot/microform level from a diverse array of sites. Our analysis demonstrates that smartphones are capable of tracking peatland phenology by capturing variations in greenness index across changing seasons. Such plot-scale phenology, particularly for the small-statured keystone peatland species such as *Sphagnum*, cannot be observed using more traditional, satellite-based methods (Hufkens *et al* 2019). Although advances in unmanned aerial vehicle technology means high resolution imagery (<5 cm) can be collected for these vegetation communities, it is still likely to be more costly and time-consuming than using the smartphone methodology we present here. We therefore recommend using a combination of these methodologies at different scales. Furthermore, connecting GLP using this readily available methodology to other time series data such as eddy covariance-based measurements of net ecosystem exchange could also help upscale phenology at sites that do not have eddy covariance towers but have resources for photo-based analyses as a low-cost alternative to the Phenocam platform (Richardson *et al* 2018). Our analysis focuses on spatial differences across sites, but with future additional data, our database can enable a better understanding of interannual variability in phenology at sites and on-going response to climate warming.

Peatlands have been subject to widespread historical (Fluet-Chouinard *et al* 2023) and ongoing drainage and degradation (Page *et al* 2022), rewetting and restoration (Andersen *et al* 2017), grazing (Valdés-Barrera *et al* 2019), climate disturbances such as warming (Müller and Joos 2021) and permafrost thaw (Varner *et al* 2022). Long-term monitoring is key to understanding how these perturbations affect



peatland functioning, but this is typically expensive and difficult to implement (Minasny *et al* 2024). Smartphone photographs offer a viable, low-cost and simple method that can be used by researchers, practitioners, and community scientists alike, to track these long-term changes by recording GLP. Furthermore, GLP can be directly related to peatland C flux (Peichl *et al* 2015, Järveoja *et al* 2018, Davidson *et al* 2021) and thus this method could be combined with methods that offer ecosystem scale insights (such as optical remote sensing) to capture both community and ecosystem responses, including canopy changes that are missed with ground-based photography, to estimate multi-year C dynamics.

#### 4.3. Limitations

However, we note that there are some uncertainties with the methods used in this study. Despite using a greenness index that is robust to differing lighting conditions (Sonnentag *et al* 2012), we acknowledge that the use of different sensors used to collect photographs may impact the greenness values measured. As mentioned previously, we do not compare the absolute values of greenness among sites, rather we have focused on comparing DOY at peak greenness. Furthermore, some participants sent photos weekly across the summer, while others were sent on bi-weekly or monthly intervals. We advise researchers who wish to use this methodology in their own research to use the same sensor each time they take a photograph of their plots (see the PeatPic Protocol for more details). Last but not the least, as is the case in all studies attempting to draw general conclusions across broad regions with limited data, we acknowledge that our sites have limited coverage compared to the global distribution of northern peatlands. As such, the GLP drivers that we identified are biased to the environmental conditions found in the sites that we happened to have data from.

## 5. Conclusions

Our low cost and low effort smartphone photography method offers various proxies of peatland GLP, and additional future research opportunities to understand peatland phenology beyond just greenness. Our study suggests that latitude, surface net solar radiation, peatland type, and vegetation type can predict leaf greening patterns across global peatlands. GLP has implications for C fixation in peatlands and therefore could influence future peatland carbon sink capacity. These results can help us understand responses of peatland ecosystem functions to future environmental change. Lastly, better refining patterns of peatland GLP will also help refine parameters of Earth system models that

currently either do not parametrise peatlands or use simplistic phenology functions taken from upland systems.

## Data availability

The data and code supporting this study will be made available via the Dryad Digital Repository: DOI: <https://doi.org/10.5061/dryad.cz8w9gigp>.

## Acknowledgment

Many of the peatlands in this study are located on the traditional lands of Indigenous peoples, and we respectfully acknowledge their enduring connection to these territories. We thank Ben Bond-Lamberty for analytical advice and to Ralph Fyfe and Sophie Fauset for providing useful comments on the manuscript. Avni Malhotra acknowledges support from NASA Terrestrial Ecology Program (Grant 80NSSC22K1253) and the Swiss National Science Foundation (project 200021\_215214). Vytas Huth acknowledges funding through the Federal Action Plan on Nature-based Solutions for Climate and Biodiversity (ANK) by the Federal Ministry for the Environment, Climate Action, Nature Conservation and Nuclear Safety (Project “OptiMuM”, grant number 3522NK1501). Mike Peacock acknowledges funding from Formas [Grant 2020-00950]. Gustaf Granath acknowledges funding from Formas 2022-02106. Emma Duley acknowledges funding from the Natural Environment Research Council and the ARIES Doctoral Training Partnership [Grant No. NE/S007334/1]. Elena Aitova acknowledges funding from the Care-Peat Project (INTERREG VB NWE 808). Antonia Hartmann and Matthias Peichl acknowledge funding from the Swedish Research Council (VR, Grant #2019-04676) and financial support to the Degerö site from VR and contributing research institutes via the national infrastructures SITES and ICOS-Sweden. Janna M Barel and Vincent E J Jassey acknowledge funding by the French National Research Agency (MIXOPEAT project, Grant No. ANR-17-CE01-0007 to VEJJ) and the Syndicat Forestier of Cournozouls for giving the access to the site of Cournozouls and help of Anna Sytiuk with fieldwork. Work at the Heathy Spur site (Australia) was conducted under Permit No. 10008289, issued by the (Victorian) Department of Environment, Land, Water and Planning (DELWP). Melanie Bird acknowledges the assistance of Ryan O'Neill with fieldwork. Jorge Perez-Quezada acknowledges Emelinda Gómez for doing the fieldwork and the financial support from ANID-Chile through Grants FONDECYT 1251027, FONDEQUIP AIC-37, PIA/BASAL FB210006 and PIA/BASAL FB210018. We thank Jerry Moore for help with figure 1.

## Author contributions

Scott J Davidson  [0000-0001-8327-2121](#)

Conceptualization (lead), Formal analysis (equal), Investigation (equal), Methodology (equal), Project administration (equal), Supervision (equal), Validation (equal), Visualization (equal), Writing – original draft (lead), Writing – review & editing (equal)

Avni Malhotra  [0000-0002-7850-6402](#)

Formal analysis (equal), Investigation (equal), Validation (equal), Visualization (equal), Writing – original draft (equal), Writing – review & editing (equal)

Vincent E J Jassey  [0000-0002-1450-2437](#)

Formal analysis (equal), Writing – review & editing (equal)

Maria Strack  [0000-0002-8996-7271](#)

Data curation (equal), Writing – review & editing (equal)

Elena Aitova  [0000-0003-1424-0868](#)

Data curation (equal), Writing – review & editing (equal)

Russell Anderson  [0000-0003-3393-8786](#)

Data curation (equal), Writing – review & editing (equal)

Lindsey J Atkinson  [0000-0001-7722-3710](#)

Data curation (equal), Writing – review & editing (equal)

Janna M Barel  [0000-0001-8520-8289](#)

Data curation (equal), Writing – review & editing (equal)

Melanie Bird  [0000-0001-7511-9514](#)

Data curation (equal), Writing – review & editing (equal)

Clarisse Brehier

Data curation (equal), Writing – original draft (equal)

Gillian Donaldson-Selby  [0000-0001-5859-5236](#)

Data curation (equal), Writing – review & editing (equal)

Emma Duley  [0000-0002-1306-5968](#)

Data curation (equal), Writing – review & editing (equal)

Joel Eklof  [0000-0003-4840-834X](#)

Data curation (equal), Writing – review & editing (equal)

Elvira de Eyto  [0000-0003-2281-2491](#)

Data curation (equal), Writing – review & editing (equal)

Gustaf Granath  [0000-0002-3632-9102](#)

Data curation (equal), Writing – review & editing (equal)

Alanna Grant  [0009-0005-7203-3260](#)

Data curation (equal), Writing – review & editing (supporting)

Antonia Hartmann  [0000-0003-1992-1742](#)

Data curation (equal), Writing – review & editing (equal)

Aleicia Holland  [0000-0001-9418-2252](#)

Data curation (equal), Writing – review & editing (equal)

Vytas Huth  [0000-0003-0615-7415](#)

Data curation (equal), Writing – review & editing (equal)

Cheristy P Jones  [0009-0006-5468-8674](#)

Data curation (equal), Writing – review & editing (equal)

Sung-Ching Lee  [0000-0002-2615-2040](#)

Data curation (equal), Writing – review & editing (equal)

Javier Lopatin  [0000-0002-5540-7428](#)

Data curation (equal), Writing – review & editing (equal)

Alice M Milner  [0000-0001-6882-3992](#)

Data curation (equal), Writing – review & editing (equal)

Mike Peacock  [0000-0002-3086-2854](#)

Data curation (equal), Writing – review & editing (equal)

Matthias Peichl  [0000-0002-9940-5846](#)

Data curation (equal), Writing – review & editing (equal)

Jorge F Perez-Quezada  [0000-0002-0449-7654](#)

Data curation (equal), Writing – review & editing (equal)

Clarice R Perryman  [0000-0002-5086-6684](#)

Data curation (equal), Writing – review & editing (equal)

Amy Pickard  [0000-0003-1069-3720](#)

Data curation (equal), Writing – review & editing (supporting)

Helena Rautakoski  [0000-0002-5297-286X](#)

Data curation (equal), Writing – review & editing (equal)

Anna-Maria Virkkala  [0000-0003-4877-2918](#)

Data curation (equal), Writing – review & editing (equal)

Emma Wegener  [0009-0002-8806-3091](#)

Data curation (equal), Writing – review & editing (equal)

## References

- Aerts R, Wallen B O and Malmer N 1992 Growth-limiting nutrients in Sphagnum-dominated bogs subject to low and high atmospheric nitrogen supply *J. Ecol.* **80** 131–40
- Andersen R, Farrell C, Graf M, Muller F, Calvar E, Frankard P, Caporn S and Anderson P 2017 An overview of the progress and challenges of peatland restoration in Western Europe *Restor. Ecol.* **25** 271–82
- Antala M, Juszczack R, van der Tol C and Rastogi A 2022 Impact of climate change-induced alterations in peatland vegetation phenology and composition on carbon balance *Sci. Total Environ.* **827** 154294
- Barve V V *et al* 2020 Methods for broad-scale plant phenology assessments using citizen scientists' photographs *Appl. Plant Sci.* **8** 311315
- Bigler C and Bugmann H 2018 Climate-induced shifts in leaf unfolding and frost risk of European trees and shrubs *Sci. Rep.* **8** 9865
- Blodau C 2002 Carbon cycling in peatlands A review of processes and controls *Environ. Rev.* **10** 111–34
- Charman D J *et al* 2013 Climate-related changes in peatland carbon accumulation during the last millennium *Biogeosciences* **10** 929–44
- Chavent M, Simonet V K, Liquet B and Saracco J 2012 ClustOfVar: an R package for the clustering of variables *J. Stat. Softw.* **50** 1–16
- Collins C G *et al* 2021 Experimental warming differentially affects vegetative and reproductive phenology of tundra plants *Nat. Commun.* **11** 3442
- Crichton K A, Anderson K, Charman D J and Gallego-Sala A 2022 Seasonal climate drivers of peak NDVI in a series of Arctic peatlands *Sci. Total Environ.* **838** 156419
- Crimmins M A and Crimmins T M 2008 Monitoring plant phenology using digital repeat photography *Environ. Manage.* **41** 949–58
- Davidson S J, Davies M A, Wegener E, Claussen S, Schmidt M, Peacock M and Strack M 2024 Carbon stocks and fluxes from a boreal conifer swamp: filling a knowledge gap for understanding the boreal C cycle *JGR Biogeosci.* **129** e2024JG008005
- Davidson S J, Good E M, Malhotra A, Estey C O, Korsah P and Strack M 2021 Linear disturbances shift boreal peatland plant species communities toward earlier peak greenness *J. Geophys. Res.* **126** e2021JG006403
- Denham S O, Barnes M L, Chang Q, Korolev M, Wood J D, Oishi C, Shay K O, Stoy P C, Chen J and Novick K A 2023 The rate of canopy development modulates the link between the timing of spring leaf emergence and summer moisture *J. Geophys. Res.* **128** e2022JG007217
- Estiarte M and Peñuelas J 2014 Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency *Glob. Change Biol.* **21** 1005–7
- Fang H, Beret F, Plummer S and Schaepman-Strub G 2019 An overview of global leaf area index (LAI): methods, products, validation, and applications *Rev. Geophys.* **57** 739–99
- Filippa G *et al* 2016 Phenopix: a R package for image-based vegetation phenology *Agric. For. Meteorol.* **220** 141–50
- Fluet-Chouinard E *et al* 2023 Extensive global wetland loss over the past three centuries *Nature* **614** 281–6
- Gallego-Sala A V *et al* 2018 Latitudinal limits to the predicted increase of peatland carbon sink with warming *Nat. Clim. Change* **8** 907–13
- Garisoain R, Delire C, Decharme B, Ferrant S, Granouillac F, Payre-Suc V and Gandois L 2023 A study of dominant vegetation phenology in a Sphagnum mountain peatland using *in situ* and Sentinel-2 observations *J. Geophys. Res.* **128** e2023JG007403
- Girkin N T and Davidson S J 2024 Protect peatlands to achieve climate goals *Science* **383** 490
- Griffiths N A *et al* 2017 Temporal and spatial variation in peatland carbon cycling and implications for interpreting responses of an ecosystem-scale warming experiment *Soil Sci. Soc. Am. J.* **81** 1668–88
- Gu Y *et al* 2023 The underappreciated importance of solar radiation in constraining spring phenology of temperate ecosystems in the Northern and Eastern United States *Remote Sens. Environ.* **294** 113617
- Gutekunst C, Koebsch F, Beyer F, Günther A, Jacobs O, Jansen F, Jurasinski G, Köhn D and Huth V 2019. Using plot-scale greenness to monitor vegetation development and model CO<sub>2</sub> exchange in peatland restoration trials *European Geosciences Union Annual Meeting*
- Hanson P J *et al* 2020 Rapid net carbon loss from a whole-ecosystem warmed peatland *AGU Adv.* **1** e2020AV00163
- Hijmans R 2024 Terra: spatial data analysis *R package version* pp 1.7–78 (available at: <https://CRAN.R-project.org/package=terra>)
- Hudson A R, Smith W K, Moore D J P and Trouet V 2022 Length of growing season is modulated by Northern hemisphere jet stream variability *Int. J. Climatol.* **42** 5644–60
- Hufkens K, Friedl M, Sonnentag O, Braswell B H, Milliman T and Richardson A D 2012 Linking near-surface and satellite remote sensing measurements of deciduous broadleaf forest phenology *Remote Sens. Environ.* **117** 307–21
- Hufkens K, Melaas E K, Mann M L, Foster T, Ceballos F, Robles M and Kramer B 2019 Monitoring crop phenology using a smartphone based near-surface remote sensing approach *Agric. For. Meteorol.* **265** 327–37
- Huth V *et al* 2021 The climate benefits of topsoil removal and *Sphagnum* introduction in raised bog restoration *Restor. Ecol.* **30** e13490
- Järveoja J, Nilsson M B, Gažovič M, Crill P M and Peichl M 2018 Partitioning of the net CO<sub>2</sub> exchange using an automated chamber system reveals plant phenology as key control of production and respiration fluxes in a boreal peatland *Glob. Change Biol.* **24** 3436–51
- Keuper F, van Bodegom P M, Dorrepaal E, Weedon J T, van Hal J, van Logtesijn R S P and Aerts R 2012 A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands *Glob. Change Biol.* **18** 1998–2007
- Kivimäki S K, Yli-petäys M and Tuittila E S 2008 Carbon sink function of sedge and Sphagnum patches in a restored cut-away peatland: increased functional diversity leads to higher production *J. Appl. Ecol.* **45** 921–9
- Klinger Y P, Eckstein R L and Kleinebecker T 2023 iPhenology: using open-access citizen science photos to track phenology at continental scale *Methods Ecol. Evol.* **14** 1424–31
- Koebsch F *et al* 2020 Refining the role of phenology in regulating gross ecosystem productivity across European peatlands *Glob. Change Biol.* **26** 867–87
- Köster E, Chapman J P B, Barrel J M, Korrensalo A, Laine A M, Vasander H T and Tuittila E-S 2023 Water level drawdown makes boreal peatland vegetation more responsive to weather conditions *Glob. Change Biol.* **29** 5691–705
- Lai J *et al* 2024 Evaluating the relative importance of predictors in Generalized Additive Models using the gam.hp R package *Plant Divers.* **46** 542–546
- Laine A M, Korrensalo A, Kokkonen N A K and Tuittila E-S 2021 Impact of long-term water level drawdown on functional plant trait composition of northern peatlands *Funct. Ecol.* **35** 2342–57
- Leonard R, Moore P, Krause S, Devito K J, Petron G R, Mendoza C, Waddington J M and Kettridge N 2021 The influence of system heterogeneity on peat-surface temperature dynamics *Environ. Res. Lett.* **16** 024002
- Leppälä M, Kukko-Oja K, Laine J and Tuittila E S 2008 Seasonal dynamics of CO<sub>2</sub> exchange during primary succession of

- boreal mires as controlled by phenology of plants *Ecoscience* **15** 460–71
- Letendre H, Poulin M and Rochefort L 2008 Sensitivity of spectral indices to CO<sub>2</sub> fluxes for several plant communities in a *Sphagnum*-dominated peatland *Can. J. Remote Sens.* **34** S414–S425
- Liu Z, Liu K, Zhang J, Yan C, Lock T R, Kallenbach R L and Yuan Z 2022 Fractional coverage rather than green chromatic coordinate is a robust indicator to track grassland phenology using smartphone photography *Ecol. Inform.* **68** 101544
- Minasny B *et al* 2024 Mapping and monitoring peatland conditions from global to field scale *Biogeochemistry* **167** 383–425
- Moore T R, Roulet N T and Waddington J M 1998 Uncertainty in predicting the effects of climatic change on the carbon cycling of Canadian peatlands *Clim. Change* **40** 229–45
- Müller J and Joo F 2021 Committed and projected future changes in global peatlands—continued transient model simulations since the last glacial maximum *Biogeosciences* **18** 3657–87
- Munir T M, Perkins M, Kaing E and Strack M 2015 Carbon dioxide flux and net primary production of a boreal treed bog: responses to warming and water-table-lowering simulations of climate change *Biogeosciences* **12** 1091–1011
- Muñoz Sabater J 2019 ERA5-land monthly averaged data from 1950 to present. Copernicus climate change service (C3S) climate data store (CDS) (<https://doi.org/10.24381/cds.68d2bb30>) (Accessed 20 July 2023)
- Page S E, Rieley J O and Banks C J 2011 Global and regional importance of the tropical peatland carbon pool *Glob. Change Biol.* **17** 798–818
- Page S *et al* 2022 Anthropogenic impacts on lowland tropical peatland biogeochemistry *Nat. Rev. Earth Environ.* **3** 426–43
- Peacock M *et al* 2019 The full carbon balance of a rewetted cropland fen and a conservation-managed fen *Agric. Ecosyst. Environ.* **269** 1–12
- Peichl M, Gažovič M, Vermeji I, de Goede E, Sonnentag O, Limpens J and Nilsson M B 2018 Peatland vegetation composition and phenology drive the seasonal trajectory of maximum gross primary production *Sci. Rep.* **8** 8012
- Peichl M, Sonnentag O and Nilsson M B 2015 Bringing colour into the picture: using digital repeat photography to investigate phenology controls of the carbon dioxide exchange in a boreal mire *Ecosystems* **18** 115–31
- R Core Team 2024 R: A language and environment for statistical computing (R Foundation for Statistical Computing) (available at: <https://www.R-project.org/>)
- Reichstein M *et al* 2019 Deep learning and process understanding for data-driven Earth system science *Nature* **566** 195–204
- Ren Y, Qiu J, Zeng Z, Liu X, Sitch S, Pilegaard K, Yang T, Wang S, Yuan W and Jain A K 2024 Earlier spring greening in Northern hemisphere terrestrial biomes enhanced net ecosystem productivity in summer *Commun. Earth Environ.* **5** 122
- Richardson A D *et al* 2018 Tracking vegetation phenology across diverse North American biomes using PhenoCam imagery *Sci. Data* **5** 180028
- Riquelme Del Río B, Sepulveda-Jauregui A, Salas-Rabaza J A, Mackenzie R and Thalasso F 2024 Fine-scale spatial variability of greenhouse gas emissions from a subantarctic peatland bog *Environ. Sci. Technol.* **58** 7393–402
- Saunois M *et al* 2025 Global methane budget 2000–2020 *Earth Syst. Sci. Data* **17** 1873–958
- Schädel C, Seydinasrollah B, Hanson P J, Hufkens K, Pearson K J, Warren J M and Richardson A D 2023 Using long-term data from a whole ecosystem warming experiment to identify best spring and autumn phenology models *Plant-Environ. Interact.* **4** 188–200
- Scharlemann J P W, Tanner E V J, Hiederer R and Kapos V 2014 Global soil carbon: understanding and managing the largest terrestrial carbon pool *Carbon Manage.* **5** 81–91
- Simpson G, Wade T, Helfter C, Jones M R, Yeung K and Nichol C J 2025 Inter-annual variability of peatland vegetation captured using phenocam-and UAV imagery *Remote Sens.* **17** 526
- Sonnentag O, Hufkens K, Teshera-Sterne C, Young A M, Friedl M, Braswell B H, Milliman T, O'Keefe J and Richardson A D 2012 Digital repeat photography for phenological research in forest ecosystems *Agric. For. Meteorol.* **152** 159–77
- Strack M, Davidson S J, Hirano T and Dunn C 2022 The potential of peatlands as nature-based climate solutions *Curr. Clim. Change Rep.* **8** 71–82
- Strack M and Waddington J M 2007 Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment *Glob. Biogeochem. Cycles* **21** GB1007
- Ström L, Mastepanov M and Christensen T R 2005 Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands *Biogeochemistry* **75** 65–82
- Thayamkottu S, Smallman T L, Pärn J, Mander Ü, Euskirchen E S and Kane E S 2024 Greening of a boreal rich fen driven by CO<sub>2</sub> fertilisation *Agric. For. Meteorol.* **359** 110261
- Tonnang H E Z, Balemi T, Masuki K F, Mohammed I, Adewopo J, Adnan A A, Mudereri B T, Vanlauwe B and Craufurd P 2020 Rapid acquisition, management, and analysis of spatial Maize (*Zea mays* L.) phenological data—towards 'big data for agronomy transformation in Africa *Agronomy* **10** 1363
- Toomey M *et al* 2015 Greenness indices from digital cameras predict the timing and seasonal dynamics of canopy-scale photosynthesis *Ecol. Appl.* **25** 99–115
- Valdés-Barrera A, Kutzbach L, Celis-Diez J L, Armesto J J, Holl D and Perez-Quezada J F 2019 Effects of disturbance on the carbon dioxide balance of an anthropogenic peatland in northern Patagonia *Wetlands Ecol. Manage.* **27** 635–50
- van Bellen S and Larivière V 2020 The ecosystem of peatland research: a bibliometric analysis *Mires Peat* **26** 15
- van der Molen P, Schalkoort M and Smit R 1994 Vegetation and ecology of hummock-hollow complexes on an Irish raised bog *Biol. Environ. Proc. R. Irish Acad.* **94B** 145–75 (available at: <http://www.jstor.org/stable/20499927>)
- van der Velde Y *et al* 2021 Emerging forest-peatland bistability and resilience of European peatland carbon stores *Proc. Natl Acad. Sci.* **118** e2101742118
- Varner R K, Crill P M, Frolking S, McCalley C K, Burke S A, Chanton J P, Holmes M E, Saleska S and Palace M W 2022 Permafrost thaw driven changes in hydrology and vegetation cover increase trace gas emissions and climate forcing in Stordalen Mire from 1970 to 2014 *Phil. Trans. R. Soc. A* **380** 20210022
- Villa J A, Mejía G M, Velásquez D, Botero A, Acosta S A, Marulanda J M, Osorno A M and Bohrer G 2019 Carbon sequestration and methane emissions along a microtopographic gradient in a tropical Andean peatland *Sci. Total Environ.* **654** 651–61
- Walther S, Guanter L, Heim B, Jung M, Duveiller G, Wolanin A and Sachs T 2018 Assessing the dynamics of vegetation productivity in circumpolar regions with different satellite indicators of greenness and photosynthesis *Biogeosciences* **15** 6221–56
- Wingate L *et al* 2015 Interpreting canopy development and physiology using a European phenology camera network at flux sites *Biogeosciences* **12** 5995–6015
- Wood S N 2011 Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models *J. R. Stat. Soc. B* **73** 3–36
- Yu Z C 2012 Northern peatland carbon stocks and dynamics: a review *Biogeosciences* **9** 4071–85