# **ENVIRONMENTAL RESEARCH**





#### **ACCEPTED MANUSCRIPT • OPEN ACCESS**

# The PeatPic Project: Predicting plot-scale peatland green leaf phenology across global peatlands

To cite this article before publication: Scott J Davidson et al 2025 Environ. Res. Lett. in press https://doi.org/10.1088/1748-9326/ae0658

# Manuscript version: Accepted Manuscript

Accepted Manuscript is "the version of the article accepted for publication including all changes made as a result of the peer review process, and which may also include the addition to the article by IOP Publishing of a header, an article ID, a cover sheet and/or an 'Accepted Manuscript' watermark, but excluding any other editing, typesetting or other changes made by IOP Publishing and/or its licensors"

This Accepted Manuscript is © 2025 The Author(s). Published by IOP Publishing Ltd.

As the Version of Record of this article is going to be / has been published on a gold open access basis under a CC BY 4.0 licence, this Accepted Manuscript is available for reuse under a CC BY 4.0 licence immediately.

Everyone is permitted to use all or part of the original content in this article, provided that they adhere to all the terms of the licence <a href="https://creativecommons.org/licences/by/4.0">https://creativecommons.org/licences/by/4.0</a>

Although reasonable endeavours have been taken to obtain all necessary permissions from third parties to include their copyrighted content within this article, their full citation and copyright line may not be present in this Accepted Manuscript version. Before using any content from this article, please refer to the Version of Record on IOPscience once published for full citation and copyright details, as permissions may be required. All third party content is fully copyright protected and is not published on a gold open access basis under a CC BY licence, unless that is specifically stated in the figure caption in the Version of Record.

View the article online for updates and enhancements.

# The PeatPic Project: Predicting plot-scale peatland green leaf phenology across

2 global peatlands

- 4 Scott J. Davidson<sup>1,2,3†\*</sup>, Avni Malhotra<sup>4\*</sup>, Vincent E.J. Jassey<sup>5</sup>, Maria Strack<sup>2</sup>, Elena Aitova<sup>6</sup>,
- 5 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
- 6 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
- 7 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.
- 8 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
- 9 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
- 10 Rautakoski<sup>30</sup>, Ewen Silvester<sup>3</sup>, Anna-Maria Virkkala<sup>31,32</sup>, Emma Wegener<sup>2</sup>

12 Corresponding author: Scott J. Davidson sjdavidson989@gmail.com

14 \*Joint first author

- 16 <sup>1</sup> School of Geography, Earth and Environmental Sciences, University of Plymouth, UK
- 17 <sup>2</sup> Department of Geography and Environmental Management, University of Waterloo,
- 18 Canada
- 19 <sup>3</sup> Department of Ecological, Plant and Animal Sciences, La Trobe University,
- 20 Albury/Wodonga, VIC, Australia
- <sup>4</sup> Biological Sciences Division, Pacific Northwest National Laboratory, USA
- <sup>5</sup> Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de
- 23 Toulouse, CNRS, IRD, Toulouse INP, 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, Scottish Borders, UK
- <sup>8</sup> Forest Research, Roslin, Midlothian, UK
- 27 <sup>9</sup> School of Environmental Sciences, University of Hull, United Kingdom
- 28 <sup>10</sup> Ecology & Biodiversity, Institute of Environmental Biology, Department of Biology, Faculty
- 29 of Science, Utrecht University, The Netherlands
- 30 <sup>11</sup> University of Applied Sciences Weihenstephan-Triesdorf, Germany
- 31 <sup>12</sup> James Hutton Institute, Aberdeen, Scotland
- 32 <sup>13</sup> Civil and Environmental Engineering, University of Washington, USA
- 33 <sup>14</sup> Department of Environmental Studies and Sciences, University of Puget Sound, USA
- 34 <sup>15</sup> Marine Institute, Furnace, Newport, Co. Mayo, Ireland
- 35 <sup>16</sup> Department of Ecology and Genetics, EBC, Uppsala University, Sweden
- 36 <sup>17</sup> UK Centre for Ecology & Hydrology, Edinburgh, Bush Estate, Penicuik, Midlothian, UK

<sup>18</sup> Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden <sup>19</sup> Peatland Science, Institute for Botany and Landscape Ecology, University of Greifswald, Germany, Partner in the Greifswald Mire Centre <sup>20</sup> Department of Earth Sciences and the Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH. USA <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, UK <sup>24</sup> Department of Geography and Planning, School of Environmental Science, University of Liverpool, UK <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, USA <sup>30</sup> Finnish Meteorological Institute, Helsinki, Finland <sup>31</sup> Woodwell Climate Research Center, Falmouth, MA, USA <sup>32</sup> Department of Geosciences and Geography, University of Helsinki, Finland <sup>†</sup> Now at: Département des sciences biologiques, Université du Québec à Montréal, Montréal, Canada **Abstract** 

Peatlands store approximately one-third of the world's soil carbon (C), but their functioning is highly variable at small 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—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 green leaf phenology (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, such as day of year at peak greenness, varied significantly across peatland types and dominant vegetation communities, with 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 green leaf phenology. 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 green leaf phenology, 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 disportionately 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; Scharlemann et al. 2014; Yu, 2012). 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. 2024). 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; Simpson et al. 2025; Köster et al, 2023). 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 (Collins et al. 2021; Richardson et al. 2018). 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 green leaf phenology of understory plants and its variation across northern peatlands remains elusive.

Changes in green leaf phenology can have significant impacts on net annual C uptake (Koebsch et al. 2020; Hanson 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 & 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 submeter 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 (≤1 m²) 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-meter 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. 2024) 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 hypothesize 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 to 1 m²) 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 Red-Green-Blue photography analysis

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

204 Greenness index =  $G_{DN} / R_{DN} + G_{DN} + B_{DN}$  Eq. 1

where the  $R_{DN}$ ,  $G_{DN}$  and  $B_{DN}$  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. 2019). 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):

Modelled greenness index =  $a \times e^{-0.5} [DOY - \frac{b}{c}]^2$  Eq. 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 eq. 2 when p-value <0.05. Out of our total 319 plot-years where we fit the eq. 2 model, we had to remove 96 unique plot-years because their model fit p-value was >0.05. Note that to standardize 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 eq. 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 February 18, 2025). The resolution of the ERA5 data is 0.25° x 0.25°. 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 (GAMM) 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 1,000 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 1,000 iterations (highest Tes-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* to assess the partition of variance explained by each predictor in our best GAMM model.

Table 1. Predictor variables included in the Generalized Mixed Effects Additive Models (GAMM).

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

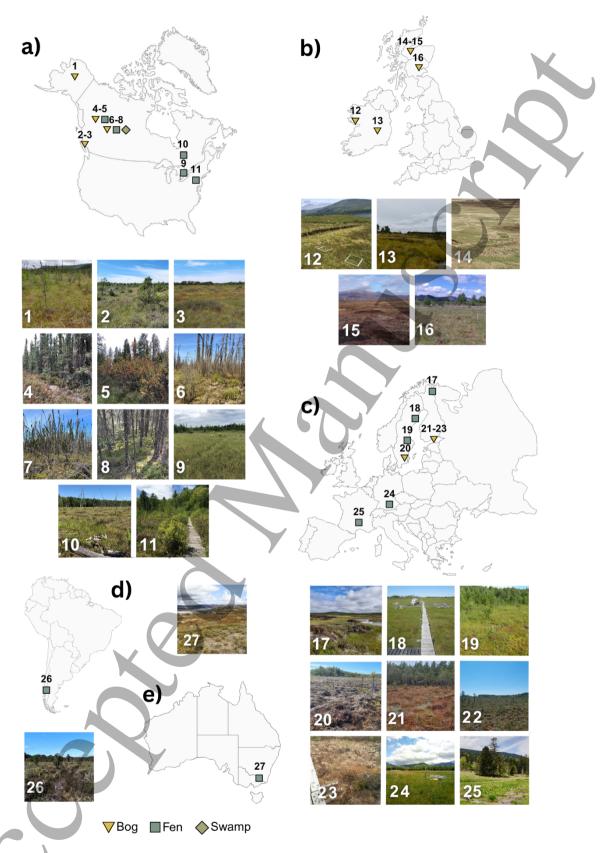
Dominant Vegetation type	Indicates the dominant vegetation type in the plot	Shrub, Sphagnum, feather moss or graminoid dominated	Site PI reported	Plant taxonomic groups have varying phenological traits
Microform	Indicates where plot was located on the landscape	Hummock, hollow or lawn	Site PI reported	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 meters per cubic meter (m³/m³)	Climate reanalysis (ERA5)	Impacts plant moisture and nutrient availability, affecting the timing of peak vegetation health.
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	Meters (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 meter (J m <sup>-2</sup> )	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 meter (J m <sup>-2</sup> )	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 meter (J m <sup>-2</sup> )	Climate reanalysis (ERA5)	Affects microclimatic conditions, influencing plant metabolism and the timing of peak vegetation greenness.

#### 3. Results

# 3.1 Description of collected data

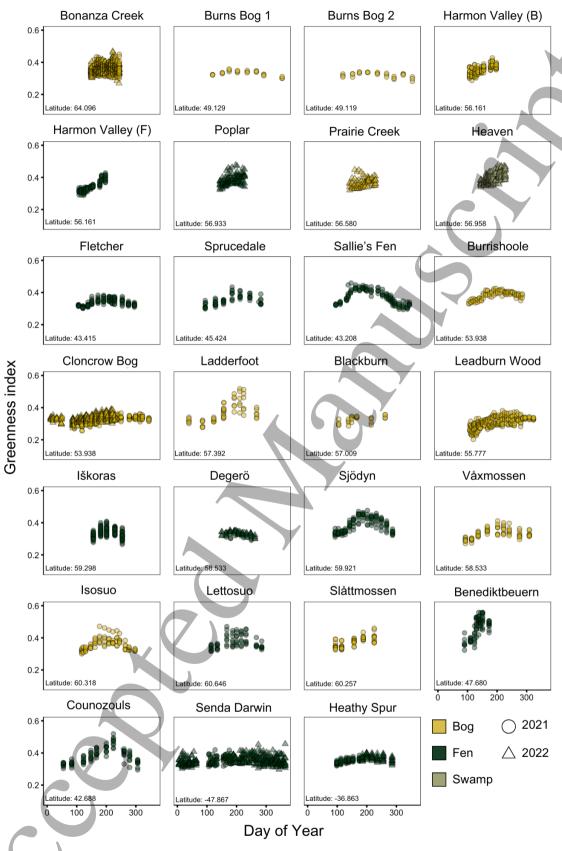
In total, over 3,700 photographs (2433 in 2021 and 1306 in 2022) were contributed to this project from participants across 164 unique plots distributed among 27 different sites in 10 different countries (Figure 1/Table S1). Most photographs were collected from bogs (11 open and 3 with trees) and fens (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 graminoiddominated (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 ± 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 plotyear (Methods in section 2.2).





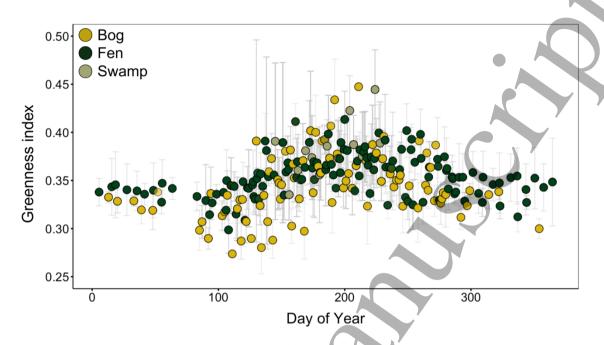
**Figure 1**. Location and photographs of study sites: 1) Bonanza Creek (\*), 2) Burns Bog 1 (\*), 3) Burns Bog 2 (\*), 4) Harmon Valley (\*), 5) Harmon Valley (\*\*), 6) Poplar (\*\*), 7) Prairie Creek (\*), 8) Heaven (\*\*\*), 9) Fletcher (\*\*), 10) Sprucedale (\*\*), 11) Sallie's Fen (\*\*), 12) Burrishoole (\*), 13) Cloncrow (\*),

14) Ladderfoot (\*), 15) Blackburn (\*), 16) Leadburn Wood (\*), 17) Iškoras (\*\*), 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 eq. 2 in methods).

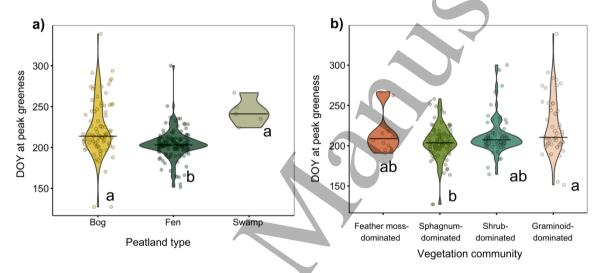


**Figure 3**. Mean  $\pm$  SE greenness index for plots across all 27 sites (coloured by peatland type, bog n = 145, fen n = 154 and swamp n = 14), averaged by day of year. The southern hemisphere day of the year has been adjusted to match the northern hemisphere (see Methods).



3.2 Variability in green leaf phenology

Day of year at peak greenness was significantly different between peatland types (Figure 4A; 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 days 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 4B; 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.

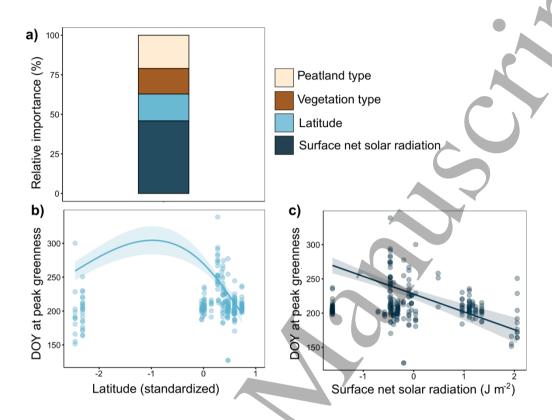


**Figure 4**. a) Day of year (DOY) at peak greenness for all three peatland types (each point represents a different plot) and b) for all four vegetation community types. Horizontal black bars indicate the median day of year. Lowercase letters indicate significant differences between categories (Kruskal-Wallis and pairwise comparisons using a Steel-Dwass post-hoc test. Statistical significance was set at p < 0.05 for all tests).

# 3.3 Predictors of green leaf phenology

The best GAMM had a very good predictive strength with  $R^2$  = 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) (Figure 4 and 5A). Furthermore, surface net solar radiation (46% of total deviance explained) and latitude (17% of total deviance explained) were the most important factors driving green leaf phenology across peatlands (Figure 5A-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 5C). 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 5B), while noting the difference in site distribution along latitude.



**Figure 5**. A) Variance partitioning modelling evaluating the portions of variation in green leaf phenology and response of day of year (DOY) at peak greenness to B) changing latitude and C) surface net solar radiation. The y-axis indicates the relative influence of the explanatory variables on the prediction based on partial residuals from the GAMM. Shaded area shows a 95% confidence interval while the line shows the smooth or linear trend. All continuous environmental variables shown were standardised before GAMM model fitting. The partial effects (y-axis) reflect these standardised scales (x-axis).

# 4. Discussion

Here, we investigated climatic, environmental and vegetation controls on peatland plant community green leaf phenology (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 4A), 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. 2019). 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 & 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 & 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 (UAV) 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 photobased 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 (Page et al. 2022) drainage and degradation, rewetting and restoration (Andersen et al. 2017), grazing (Valdés-Barrera et al. 2019), climate disturbances such as warming (Muller 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. 2023). 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. 2018), 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 greening. Our study suggests that latitude, surface net solar radiation, peatland type, and vegetation type can predict leaf greening patterns across global peatlands. Green leaf phenology 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 parameterize 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: 10.5061/dryad.cz8w9gjgp. Photographs will be available on our GitHub repository.

#### **Author contributions**

SJD conceived the work. MS, EA, RA, LJA, JMB, VEJJ, MB, CB, GD-S, EdE, AH, GG, AH, S-CL, AL, MPk, MPl, JFPQ, CRP, HR, ES, A-MV and EW contributed photographs for the study. SJD, AM and VEJJ conducted the analysis. All authors contributed to the interpretation of data and writing.

# **Acknowledgements**

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. 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 number 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 Counozouls for giving the access to the site of Counozouls 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.

# 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. Journal of
- *Ecology*, 131-140.

- 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. Restoration Ecology, 25(2): 271-282.

- 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.
- 568 Science of The Total Environment, 827: 154294.

- Barve, V.V., Brenskelle, L., Li, D., Stucky, B.J., Barve, B.V., Hantak, M.M., McLean, B.S.,
- Paluh, D.J., Oswald, J.A., Belitz, M.W., Folk, R.A. and Guralnick, R.P. 2020. Methods for
- 572 broad-scale plant phenology assessments using citizen scientists' photographs. *Applications*
- 573 in Plant Sciences. 8(1): 311315.

- 575 Bigler, C. and Bugmann, H. 2018. Climate-induced shifts in leaf unfolding and frost risk of
- 576 European trees and shrubs. Scientific Reports, 8: 9865.

- 578 Blodau, C. 2002. Carbon cycling in peatlands A review of processes and controls.
- 579 Environmental Reviews, 10(2): 111-134.

581 Breiman, L. 2001. Random Forests. *Machine Learning*, 45: 5-32.

- Collins, C.G., Elmendorf, S.C., Hollister, R.D., Henry, G.H.R., Clark, K., Bjorkman, A.D.,
- Myers-Smith, I.H., Prevéy, J.S., Ashton, I.W., Assman, J.J., Alatalo, J.M., Carbongnani, M.,
- Chisholm, C., Cooper. E.J., Forrester, C., Jónsdóttir, I.S., Klanderud, K., Kop, C.W.,
- Livensperger, C., Mauritz, M., May, J.L., Molau, U., Oberbauer, S.F., Ogburn, E., Panchen,
- 587 Z.A., Petraglia, A., Post, E., Rixen, C., Rodenhizer, H., Schuur, E.A.G., Semenchuk, P.,
- 588 Smith, J.G., Steltzer, H., Totlan, Ø, Walker, M.D., Welker, J.M. and Suding, K.N. 2021.
- 589 Experimental warming differentially affects vegetative and reproductive phenology of tundra
- 590 plants. Nature Communications, 11(12): 3442.

- Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M.,
- 593 Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D.M., Jackson, S.T., Korhola, A.,
- Mauguoy, D., Mitchell, F.J.G., Prentice, I.C., van der Linden, M., De Vleeschouwer, F., Yu,

- 595 Z.C., Alm, J., Bauer, I.E., Corish, Y.M.C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le
- Roux, G., Loisel, J., Moschen, R., Nichols. J.E., Nieminen, T.M., MacDonald, G.M.,
- Phadtare, N.R., Rausch, N., Sillasoo, Ü., Swindles, G.T., Tuittila, E.-S., Ukonmaanaho, L.,
- Väliranta, M., van Bellen, S., van Geel, B., Vitt, D.H. and Zhao, Y. 2013. Climate-related
- changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, 10:
- 600 929-944.
- 602 Chavent, M., Simonet, V.K., Liquet, B. and Saracco, J. 2012. CLUSTOFVAR: an R package
- for the clustering of variables. *Journal of Statistical Software*, 50:1–16.
- 605 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. Science of The Total Environment, 838:
- 607 156419.
- - 609 Crimmins, M.A. and Crimmins, T.M. 2008. Monitoring plant phenology using digital repeat
  - 610 photography. Environmental management, 41: 949-958.
- Davidson, S.J., Good, E.M., Malhotra, A., Estey, C.O., Korsah, P. and Strack. M. 2021.
- 613 Linear disturbances shift boreal peatland plant species communities toward earlier peak
- greenness. Journal of Geophysical Research: Biogeosciences, 126(8): e2021JG006403.
- - Davidson, S.J., Davies, M.A., Wegener, E., Claussen, S., Schmidt, M., Peacock, M. and
- 617 Strack, M. 2024. Carbon stocks and fluxes from a boreal conifer swamp: filling a knowledge
- gap for understanding the boreal C cycle. JGR Biogeosciences, 129(5): e2024JG008005.
- 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. Journal of
- 623 Geophysical Research: Biogeosciences, 128(4): e2022JG007217.
- 625 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. Global Change
- 627 Biology, 21(3): 1005-1007.

- 629 Fang, H., Beret, F., Plummer, S. and Schaepman-Strub, G. 2019. An Overview of Global
- 630 Leaf Area Index (LAI): Methods, Products, Validation, and Applications. Reviews of
- 631 Geophysics, 57(3): 739-799.

- 633 Filippa, G., Cremonese, E., Migliavacca, M., Galvagano, M., Forkel, M., Wingate, L., et al.
- 634 2016. Phenopix: A R package for image-based vegetation phenology. Agricultural and
- 635 Forest Meteorology, 220: 141–150.
- - Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., Malhotra, A., Melton, J.R., Poulter, B., Kaplan,
  - 638 J.O., Goldewijk, K.K., Siebert, S., Minayeva, T. and Hugelius, G. 2023. Extensive global
  - wetland loss over the past three centuries. *Nature*, 614(7947): 281-286.
- Gallego-Sala, A.V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P.,
- Moreton, S., Amesbury, M.J., Beilman, D.W., Björck, S., Blyakharchuk, T., Bochicchio, C.,
- Booth, R.K., Bunbury, J., Camill, P., Carless, D., Chimner, R.A., Clifford, M., Cressey, E.,
- 644 Courtney-Mustaphi, C., De Vleeschouwer, F., de Jong, R., Fialkiewicz-Koziel, B.,
- Finkelstein, S.A., Garneau, M., Githumbi, E., Hribjlan, J., Holmquist, J., Hughes, P.D.M.,
- Jones, C., Jones, M.C., Karofeld, E., Klein, E.S., Kokfelt, U., Korhola, A., Lacourse, T., Le
- Roux, G., Lamentowicz, M., Large, D., Lavoie, M., Loisel, J., Mackay, H., MacDonald, G.M.,
- Makila, M., Magnan, G., Marchant, R., Marcisz, K., Martínez Cortizas, A., Massa, C.,
- Mathijssen, P., Mauquoy, D., Mighall, T., Mitchell, F.J.G., Moss, P., Nichols, J., Oksanen,
- 650 P.O., Orme, L., Packalen, M.S., Robinson, S., Roland, T.P., Sanderson, N.K., Sannel,
- A.B.K., Silva-Sánchez, N., Steinberg, N., Swindles, G.T., Turner, T.E., Uglow, J., Väliranta,
- M., van Bellen, S., van der Linden, M., van Geel, B., Wang, G., Yu, Z., Zaragoza-Castells, J.
- and Zhao. Y. 2018. Latitudinal limits to the predicted increase of peatland carbon sink with
- 654 warming. Nature Climate Change, 8: 907-913.
- 656 Garisoain, R., Delire, C., Decharme, B., Ferrant, S., Granouillac, F., Payre-Suc, V. and
- 657 Gandois, L. 2023. A Study of Dominant Vegetation Phenology in a Sphagnum Mountain
- 658 Peatland Using In Situ and Sentinel-2 Observations. *Journal of Geophysical Research:*
- 659 Biogeosciences, 128(10): e2023JG007403.
- 661 Girkin, N.T. and Davidson, S.J. 2024. Protect peatlands to achieve climate goals. Science,
- 662 383(6682): 383,490-490.
- Griffiths, N.A., Hanson, P.J., Ricciuto, D.M., Iversen, C.M., Jensen, A.M., Malhotra, A.,
- McFarlane, K.J., Norby, R.J., Sargsyan, K., Sebestyen, S.D., Shi, X., Walker, A.P., Ward,
- 666 E.J., Warren, J.M. and Weston, D.J. 2017. Temporal and Spatial Variation in Peatland
- 667 Carbon Cycling and Implications for Interpreting Responses of an Ecosystem-Scale
- Warming Experiment. Soil Science Society of America Journal, 81(6): 1668-1688.

- Gutekunst, C., Koebsch, F., Beyer, F., Günther, A., Jacobs, O., Jansen, F., Jurasinksi, G.,
- Kôhn, 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*
- 673 Annual Meeting.

- 675 Gu, Y., Zhao., Y., Guo, Z., Meng, L., Zhang, K., Wang, J., Lee, C.K.F., Xie, J., Wang, Y.,
- Yan, Z., Zhang, H. and Wu, J. 2023. The underappreciated importance of solar radiation in
- 677 constraining spring phenology of temperate ecosystems in the Northern and Eastern United
- 678 States. Remote Sensing of Environment, 294: 113617.
- Hanson, P.J., Griffiths, N.A., Iversen, C.M., Norby, R.J., Sebestyen, S.D., Phillips, J.R.,
- Chanton, J.P., Kolka, R.K., Malhotra, A., Oleheiser, K.C., Warren, J.M., Shi, X., Yang, C.,
- Mao, J. and Ricciuto, D.M. 2020. Rapid Net Carbon Loss From a Whole-Ecosystem Warmed
- 683 Peatland. *AGU Advances*, 1(3): e2020AV00163.
- 685 Hijmans, R. 2024. terra: Spatial Data Analysis. R package version 1.7-78 < https://CRAN.R-
- 686 project.org/package=terra>.
- Hudson, A.R., Smith, W.K., Moore, D.J.P. and Trouet, V. 2022. Length of growing season is
- 689 modulated by Northern Hemisphere jet stream variability. International Journal of
- *Climatology*, 42(11): 5644-5660.
- Hufkens, K., Friedl, M., Sonnentag, O., Braswell, B. H., Milliman, T., & Richardson, A. D.
- 693 2012. Linking near-surface and satellite remote sensing measurements of deciduous
- broadleaf forest phenology. Remote Sensing of Environment, 117: 307–321.
- - Hufkens, K., Melaas, E.K., Mann, M.L., Foster, T., Ceballos, F., Robles, M. and Kramer, B.
- 697 2019. Monitoring crop phenology using a smartphone based near-surface remote sensing
- 698 approach. Agricultural and forest meteorology, 265: 327-337.
- Huth, V., Günther, A., Bartel, A., Gutekunst, C., Heinze, S., Hofer, B., Jacobs, O., Koebsch,
- 701 F., Rosinski, E., Tonn, C., Ullrich, K. and Jurasinski, G. 2021. The climate benefits of topsoil
- removal and Sphagnum introduction in raised bog restoration. Restoration Ecology, 30(1):
- 703 e13490.

- Järveoja, J., Nilsson, M.B., Gažovič, M., Crill, P.M. and Peichl, M., 2018. Partitioning of the
- 706 net CO 2 exchange using an automated chamber system reveals plant phenology as key
- 707 control of production and respiration fluxes in a boreal peatland. Global Change Biology,
- 708 24(8): 3436-3451.
- - 710 Keuper, F., van Bodegom, P.M., Dorrepaal, E., Weedon, J.T., van Hal, J., van Logtesijn,
  - 711 R.S.P. and Aerts, R. 2012. A frozen feast: thawing permafrost increases plant-available
  - 712 nitrogen in subarctic peatlands. *Global Change Biology*, 18(6): 1998-2007.

  - 714 Kivimäki, S.K., Yli-petäys, M. and Tuittila, E.S. 2008. Carbon sink function of sedge and
  - 715 Sphagnum patches in a restored cut-away peatland: increased functional diversity leads to
  - 716 higher production. *Journal of Applied Ecology*, 45(3): 921-929.
- - 718 Klinger, Y.P., Eckstein, R.L. and Kleinebecker, T. 2023. iPhenology: Using open-access
  - 719 citizen science photos to track phenology at continental scale. Methods in Ecology and
  - 720 Evolution, 14(6): 1424-1431.
- - Koebsch, F., Sonnentag, O., Järveoja, J., Peltoniemi, M., Alekseychik, P., Aurela, M., Arslan,
  - A.N., Dinsmore, K., Gianelle, D., Helfter, C., Jacowicz-Korzynski, M., Korrensalo, A., Leith,
  - 724 F., Linkosalmi, M., Lohila, A., Lund, M., Maddison, M., Mammarella, I., Mander, Ü,
- 725 Minkkinen, K., Pickard, A., Pullens, J.W.M., Tuittila, E-S., Nilsson, M.B. and Peichl, M. 2020.
- Refining the role of phenology in regulating gross ecosystem productivity across European
- 727 peatlands. Global Change Biology, 26: 867-887.
- 729 Köster, E., Chapman, J.P.B., Barrel, J.M., Korrensalo, A., Laine, A.M., Vasander, H.T. and
- 730 Tuittila, E.-S. 2023. Water level drawdown makes boreal peatland vegetation more
- responsive to weather conditions. *Global Change Biology*, 29(19): 5691-5705.
- 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. Functional
- *Ecology*, 35: 2342–2357.
- Leeper, R.D., Matthews, J.L., Cesarini, M.S. and Bell, J.E. 2021. Evaluation of air and soil
- 738 temperatures for determining the onset of the growing season. Journal of Geophysical
- 739 Research: Biogeosciences, 126(8): e2020JG006171.
- 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. *Environmental Research Letters*, 16: 024002.

- Leppälä, M., Kukko-Oja, K., Laine, J. and Tuittila, E.S., 2008. Seasonal dynamics of CO2
- exchange during primary succession of boreal mires as controlled by phenology of plants.
- 747 Ecoscience, 15(4): 460-471.
- Letendre, H., Poulin, M. and Rochefort, L. 2008. Sensitivity of spectral indices to CO<sub>2</sub> fluxes
- 750 for several plant communities in a Sphagnum-dominated peatland. Canadian Journal of
- 751 Remote Sensing, 34: S414-S425.
- Linkosalmi, M., Tuovinen, J-P., Nevalainen, O., Peltoniemi, M., Taniş, C.M., Arslan, A.N.,
- Rainne, J., Lohila, A., Laurila, T. and Aurela, M. 2022. Tracking vegetation phenology of
- pristing northern boreal peatlands by combining digital photography with CO<sub>2</sub> flux and
- 756 remote sensing data. *Biogeosciences*. 19(19): 4747-4765.
- Liu, Z., Liu, K., Zhang, J., Yan, C., Lock, T.R., Kallenbach, R.L. and Yuan, Z. 2022.
- 759 Fractional coverage rather than green chromatic coordinate is a robust indicator to track
- grassland phenology using smartphone photography. Ecological Informatics, 68: 101544.
- McCarter, C. P. R. & Price, J. S. 2012. Ecohydrology of *Sphagnum* moss hummocks:
- mechanisms of capitula water supply and simulated effects of evaporation. *Ecohydrology*, 7,
- 764 33–44, https://doi.org/10.1002/eco.1313.
- McPartland, M.Y., Kane, E.S., Falkowski, M.J., Kolka, R., Turetsky, M.R., Palik, B. and
- Montgomery, R.A. 2019. The response of boreal peatland community composition and NDVI
- to hydrologic change, warming, and elevated carbon dioxide. Global change biology, 25(1):
- 769 93-107.
- - 771 Minasny, B., Adetsu, D.V., Aitkenhead, M., Artz, R.R., Baggaley, N., Barthelmes, A.,
  - Beucher, A., Caron, J., Conchedda, G., Connolly, J. and Deragon, R. 2024. Mapping and
- monitoring peatland conditions from global to field scale. *Biogeochemistry*, 167(4): 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. Climatic Change, 40:
- 777 229-245.

- 779 Muñoz Sabater, J. 2019. ERA5-Land monthly averaged data from 1950 to present.
- 780 Copernicus Climate Change Service (C3S) Climate Data Store (CDS). DOI:
- 781 10.24381/cds.68d2bb30 (Accessed on 20-07-2023).

- 783 Müller, J. and Joo, F. 2021. Committed and projected future changes in global peatlands
- 784 continued transient model simulations since the last Glacial Maximum. *Biogeosciences*, 18:
- 785 3657-3687.
- Munir, T.M., Perkins, M., Kaing, E. and Strack, M. 2015. Carbon dioxide flux and net primary
- 787 production of a boreal treed bog: Responses to warming and water-table-lowering
- simulations of climate change. *Biogeosciences*, 12: 1091-1011.

- Nijp, J.J., Limpens, J., Metselaar, K., van der Zee, S.E.A.T.M., Berendse, F. and Robroek,
- 791 B.J.M. 2014. Can frequent precipitation moderate the impact of drought on peat moss
- 792 carbon uptake in northern peatlands? New Phytologist, 203: 70-80.

- Page, S.E., Rieley, J.O. and Banks, C.J. 2011. Global and regional importance of the
- 795 tropical peatland carbon pool. *Global change biology*, 17(2): 798-818.

- 797 Page, S., Mishra, S., Agus, F., Anshari, G., Dargie, G., Evers, S., Jauhiainen, J., Jaya, A.,
- 798 Jovani-Sancho, A.J., Laurén, A. and Sjögersten, S. 2022. Anthropogenic impacts on lowland
- 799 tropical peatland biogeochemistry. *Nature Reviews Earth & Environment*, 3(7): 426-443.

- Peacock, M., Gauci, V., Baird, A.J., Burden, A., Chapman, P.J., Cumming, A., Evans, J.G.,
- Grayson, R.P., Holden, J., Kaduk, J. and Morrison, R. 2019. The full carbon balance of a
- rewetted cropland fen and a conservation-managed fen. Agriculture, Ecosystems &
- 804 Environment, 269: 1-12.

- 806 Peichl, M., Sonnentag, O. and Nilsson, M.B. 2015. Bringing Colour into the Picture: Using
- 807 Digital Repeat Photography to Investigate Phenology Controls of the Carbon Dioxide
- 808 Exchange in a Boreal Mire. *Ecosystems*, 18: 115-131.

- Peichl, M., Gažovič, M., Vermeji, I., de Goede, E., Sonnentag, O., Limpens, J. and Nilsson,
- 811 M.B. 2018. Peatland vegetation composition and phenology drive the seasonal trajectory of
- 812 maximum gross primary production. *Scientific Reports*, 8: 8012.

- 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. Communications Earth & Environment, 5: 122.

- Richardson, A.D., Hufkens, K., Milliman, T., Aubrecht, D.A., Chen, M., Gray, J.M., Johnston,
- M.R., Keenan, T.F., Klosterman, S.T., Kosmala, M., Melaas, E.K., Friedl, M.A. and Frolking,
- 820 S. 2018. Tracking vegetation phenology across diverse North American biomes using
- PhenoCam imagery. Scientific Data, 5, 180028.

- 823 Riquelme del Río, B., Sepulveda-Jauregui, A., Salas-Rabaza, J.A., Mackenzie, R. and
- 824 Thalasso, F., 2024. Fine-Scale Spatial Variability of Greenhouse Gas Emissions From a
- 825 Subantarctic Peatland Bog. Environmental Science & Technology, 58(17): 7393-7402.

- 827 Saunois, M., Martinez, A., Poulter, B., Zhang, Z., Raymond, P., Regnier, P., Canadell, J. G.,
- Jackson, R. B., Patra, P. K., Bousquet, P., Ciais, P., Dlugokencky, E. J., Lan, X., Allen, G.
- H., Bastviken, D., Beerling, D. J., Belikov, D. A., Blake, D. R., Castaldi, S., Crippa, M.,
- Deemer, B. R., Dennison, F., Etiope, G., Gedney, N., Höglund-Isaksson, L., Holgerson, M.
- A., Hopcroft, P. O., Hugelius, G., Ito, A., Jain, A. K., Janardanan, R., Johnson, M. S.,
- Kleinen, T., Krummel, P., Lauerwald, R., Li, T., Liu, X., McDonald, K. C., Melton, J. R.,
- Mühle, J., Müller, J., Murguia-Flores, F., Niwa, Y., Noce, S., Pan, S., Parker, R. J., Peng, C.,
- Ramonet, M., Riley, W. J., Rocher-Ros, G., Rosentreter, J. A., Sasakawa, M., Segers, A.,
- 835 Smith, S. J., Stanley, E. H., Thanwerdas, J., Tian, H., Tsuruta, A., Tubiello, F. N., Weber, T.
- 836 S., van der Werf, G., Worthy, D. E., Xi, Y., Yoshida, Y., Zhang, W., Zheng, B., Zhu, Q., Zhu,
- Q., and Zhuang, Q. 2024. Global Methane Budget 2000–2020, Earth Syst. Sci. Data
- *Discuss.* [preprint], https://doi.org/10.5194/essd-2024-115.

- Schädel, C., Seyednasrollah, 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-Environment Interactions*, 4(4):
- 843 188-200.

- 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 Manag. 5:
- 847 81–91.

- Simpson, G., Wade, T., Helfter, C., Jones, M.R., Yeung, K. and Nichol, C.J. 2025. Inter-
- 850 Annual Variability of Peatland Vegetation Captured Using Phenocam- and UAV Imagery.
- 851 Remote Sensing, 17: 526.

- 853 Strack, M. and Waddington, J.M. 2007. Response of peatland carbon dioxide and methane
- 854 fluxes to a water table drawdown experiment. Global Biogeochemical Cycles, 21(1):
- 855 GB1007.

- Strack, M., Davidson, S.J., Hirano, T. and Dunn, C., 2022. The Potential of Peatlands as
- Nature-Based Climate Solutions. Current Climate Change Reports, 8: 71-82.

- 860 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-
- 862 82.

- Thayamkottu, S., Smallman, T.L., Pärn, J., Mander, Ü., Euskirchen, E.S. and Kane, E.S.
- 865 2024. Greening of a boreal rich fen driven by CO2 fertilisation, Agricultural and Forest
- 866 Meteorology, 359, 110261.

- Tonnang, H.E., 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(9): 1363.

- Walther, S., Guanter, L., Heim, B., Jung, M., Duveiller, G., Wolanin, A. and Sachs, T. 2018.
- 874 Assessing the dynamics of vegetation productivity in circumpolar regions with different
- satellite indicators of greenness and photosynthesis. *Biogeosciences*, 15: 6221-6256.

- Wu, Y., Xiao, P., Zhang, X., Liu, H., Dong, Y. and Feng, L. 2023. Effects of Snow Cover on
- 878 Spring Phenology Vary With Temperature Gradient Across the Pan-Arctic. Journal of
- 879 Geophysical Research: Biogeosciences, 128(4): e2022JG007183.

- Valdés-Barrera, A., Kutzbach, L., Celis-Diez, J.L., Armesto, J,J., Holl, D., Perez-Quezada, J.F.
- 882 2019. Effects of disturbance on the carbon dioxide balance of an anthropogenic peatland in
- 883 northern Patagonia. Wetlands Ecology and Management 27: 635–650.

van Bellen, S. and Larivière, V. 2020. The ecosystem of peatland research: a bibliometric analysis. *Mires and peat*, 26: 1530.

van der Molen, P., Schalkoort, M. and Smit, R. 1994. Vegetation and ecology of Hummock-Hollow complexes on an Irish raised bog. *Biology and Environment: Proceedings of the Royal Irish Academy*, 94(2), 145-175.

van der Velde, Y., Temme, A.J.A.M., Nijp, J.J. and Teuling, A.J. 2021. Emerging forest-peatland bistability and resilience of European peatland carbon stores. *PNAS*, 118 (38): e2101742118.

Varner, R. K., Crill, P.M., Frolking, S., McCalley, C.K., Burke, S.A., Chanton, J.P., Holmes M.E., Isogenie Project Coordinators, 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.38020210022.

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. *Science of the Total Environment*,
654.651-661.

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood
estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, 73(1): 3–36.

910 Yu, Z.C. 2012. Northern peatland carbon stocks and dynamics: a review. *Biogeosciences*, 911 9(10): 4071-4085.