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Engineering restoration and gaseous carbon uptake on a degraded bog: the role of *Eriophorum angustifolium* and micropropagated *Sphagnum*

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SUMMARY

Degraded peatlands are significant sources of carbon greenhouse gases (CGHG), and their recovery can make significant contributions to climate change mitigation as well as deliver biodiversity benefits. *Sphagnum* mosses are key species for northern peatland formation and re-introduction is often needed for successful ecohydrological restoration of degraded bogs, but natural sources are scarce and often protected. Micropropagated *Sphagnum* moss products (BeadaNoss®) were developed to alleviate this constraint. This research explored in detail, for the first time, the CGHG fluxes on a cut-over lowland peatland restoration site where micropropagated *Sphagnum* was introduced to an existing ‘nurse crop’ of *Eriophorum angustifolium*, and tested the influence of vegetation maturity. Ecosystem CGHG flux was measured using closed chambers at plot scale in areas of both mature and immature *E. angustifolium* with and without application of BeadaGel™ *Sphagnum*, with control plots on bare peat. Studies were conducted over two years of contrasting weather patterns. In Year 1, mean net (CO₂e) CGHG uptake on vegetated plots was -2.33 (minimum 1.55, maximum -5.55) t ha⁻¹ yr⁻¹ with increasing CGHG uptake as vegetation matured. In Year 2, gross photosynthesis reduced significantly during the 2018 summer drought resulting in a small mean net CGHG emission of 0.11 (minimum 2.21 maximum -1.22) t ha⁻¹ yr⁻¹. *Sphagnum* application within immature vegetation resulted in greater CGHG uptake in both years, but was not as beneficial within mature vegetation. CGHG emission from bare peat (3.79 t ha⁻¹ yr⁻¹ overall) showed the magnitude of avoided losses. Methane flux contributed significantly to CGHG emission but was not closely related to water table depth. Application of *Sphagnum* within *E. angustifolium* can deliver good CGHG flux results in the early stages of degraded lowland bog recovery but cannot fully mitigate vulnerability to climate change scenarios.

KEY WORDS: climate change, cottongrass, greenhouse gases, methane, peatlands

INTRODUCTION

Although peatlands cover only 3 % of Northern Hemisphere land (Gorham 1991) they are estimated to contain 500 ± 100 Gt of carbon (C) or around one third of the world’s soil carbon (Yu 2012), which is more C than in all forests globally (Joosten *et al.* 2016). However, an estimated 15 % of the world’s peatlands are drained and damaged (Joosten *et al.* 2012) making them a source of carbon dioxide (CO₂) emissions (Leifeld & Manichetti 2018) that, with peat fires, accounts for around 5 % of all anthropogenic CO₂ emissions (Crump 2017). This amounts to ~2 Gt yr⁻¹ (Joosten 2016), which was double the global CO₂ emissions from aviation at that time (Graver *et al.* 2019). Methane (CH₄) emission from peatlands is also seen as a significant contributor to climate forcing (Glatzel *et al.* 2004, van Winden *et al.* 2012, Haddaway *et al.* 2014, Turetsky *et al.* 2014), and Evans *et al.* (2017) currently estimate that natural UK

peatlands are ‘climate neutral’ owing to climate forcing of CH₄ emissions counteracting CO₂ uptake.

Peatland restoration can modify emissions of carbon greenhouse gases (CGHG; i.e. CO₂ and CH₄) (Waddington & Warner 2001, Aitova *et al.* 2023) and is seen as an achievable climate change mitigation activity (Bain *et al.* 2011, Joosten *et al.* 2012), but rapid implementation is essential to achieve the greatest benefit (Glenk *et al.* 2021). Rewetting is a key factor in encouraging the recovery of vegetation and protecting carbon stocks in degraded peatlands (Joosten *et al.* 2012, González & Rochefort 2014). Günther *et al.* (2020) explore the dichotomy between CO₂ emission from drained peatlands and the CH₄ emission from rewetted peatlands and conclude that “CH₄ radiative forcing does not undermine the climate change mitigation potential of peatland rewetting”. *Sphagnum* mosses may reduce CH₄ flux due to the presence of methanotrophic bacteria which oxidise methane for use by the plant, although this



may be temperature or water table depth (WTD) dependent (Kip *et al.* 2010, Larmola *et al.* 2010, van Winden *et al.* 2012). The optimum water table level to limit both CO₂ and CH₄ losses is reported to be 10 cm below the surface (Evans *et al.* 2021).

In the UK, the techniques and benefits of lowland peatland restoration are presently under-researched compared to upland systems (Haddaway *et al.* 2014) and there is currently a lack of data on CGHG fluxes from degraded lowland raised bogs (Evans *et al.* 2017). *Sphagnum* mosses are an intrinsic part of lowland bog formation and development in the northern hemisphere, and bioengineer the environment for continuously favourable ecohydrological conditions (van Breemen 1995, Quinty & Rochefort 2003) through chemical processes (Rydin & Jeglum 2013) and buffering against evapotranspiration (Mazziotta *et al.* 2019). The primary aim of lowland peatland restoration is to develop a *Sphagnum*-dominated acrotelm of bog vegetation that stabilises the water table, protecting current peat stocks in the short term and promoting peat and carbon accumulation in the long term (Lindsay 2010, Lucchese *et al.* 2010, Waddington *et al.* 2011, Worrall *et al.* 2011). However, the porosity of the peat surface on cutover bogs diminishes over time with no intervention due to peat shrinkage and compaction, reducing hydrological conductivity and making moisture unavailable at the surface (Price *et al.* 2003, Zając *et al.* 2018). This makes the surface hostile to seed germination and establishment of bog vegetation, particularly non-vascular plants (Renou-Wilson *et al.* 2019) and *Sphagnum* mosses (Quinty & Rochefort 2003). Additionally, there are chemical changes (Wind-Mulder *et al.* 1996) as increased humification and recalcitrance of organic matter reduces nutrient availability to support both plant and microbial communities (Andersen *et al.* 2006). Self-regeneration to a functioning and sustainable peatland is, therefore, highly unlikely (Money & Wheeler 1999, Quinty & Rochefort 2003) and intervention with active restoration, including plant re-introduction, is needed to re-establish ecohydrological functions and peat accumulation (Rochefort 2000, Chirino *et al.* 2006, Lucchese *et al.* 2010).

Natural peatlands in many areas are designated for conservation, and collection of *Sphagnum* (for introduction to restoration sites) is undesirable and prohibited (Gahlert *et al.* 2012, Caporn *et al.* 2018). *Sphagnum* is also slow to establish naturally and effective colonisation would take many years, especially in areas such as bare, extracted peatlands where few local sources exist. Therefore, rapid and sustainable methods of propagation are needed for

effective restoration in necessarily short timescales. Micropropagation Services Ltd (trading as BeadaMoss®) produce large quantities of *Sphagnum* from tiny amounts of wild-sourced material, using standard tissue-culture techniques involving plant division in a sterile, controlled environment to produce a range of products for different applications (Caporn *et al.* 2018). BeadaGel™ contains strands of developing *Sphagnum* suspended in a hydrocolloidal gel, which is applied directly to the peatland surface aiming for even areal coverage. This product contains a mixture of species from five *Sphagnum* Sections (*Acutifolia*, *Cuspidata*, *Sphagnum*, *Squarrosa* and *Subsecunda*), selected to thrive in a range of microhabitats (Atherton *et al.* 2010, Laine *et al.* 2018) across the peatland landscape. Thus, *Sphagnum* has an opportunity to grow wherever the product is placed, as each species is adapted to a particular environmental niche (from pool to hummock) where its productivity is greater than that of other species (Clymo & Hayward 1982).

In establishment phases of bog restoration, vascular plants can ‘nurse’ and promote *Sphagnum* moss growth by providing scaffolding, environmental protection and a beneficial microclimate (Ferland & Rochefort 1997, Grosvernier *et al.* 1997, Quinty & Rochefort 2003, Pouliot *et al.* 2011) while other mosses such as *Polytrichum strictum* can reduce plant displacement caused through frost heaving (Price *et al.* 2003). *Eriophorum* species are early colonisers, and perhaps the species-of-choice to nurse re-colonising *Sphagnum* moss (Pouliot *et al.* 2011, Nugent *et al.* 2018) as they provide environmental protection and help stabilise the peat surface without out-competing *Sphagnum* or smothering it with plant litter (Guêné-Nanchen *et al.* 2017). However, *Eriophorum* species have aerenchyma, which brings air to the roots and rhizosphere of wetland plants and thus also provides a direct route to the atmosphere for CH₄ from the anaerobic, waterlogged peat (Schimel 1995, Videmšek *et al.* 2006). This raises concerns that peatlands undergoing restoration may become GHG sources rather than sinks due to elevated CH₄ emissions (Lindsay 2010, Evans *et al.* 2016) in the short term, until *Sphagnum* is fully established. On the other hand, oxic conditions created in the rhizosphere of aerenchymatous plants allow methanotrophic bacteria to oxidise CH₄, which distances roots from the methane store (Fritz *et al.* 2011). On balance, the role of *Eriophorum* species may be advantageous for climate change mitigation if it facilitates successful peatland restoration.

The aims of this study were to ascertain whether rewetting and planting of *Eriophorum angustifolium*

swards with tissue-cultured *Sphagnum* moss at a degraded lowland bog delivered a carbon greenhouse gas (CGHG) sink or source, whether maturity or type of vegetation were key factors, and to develop a greater understanding of the drivers of gaseous carbon flow to inform future site management. The hypotheses were that:

1. restoration of the site will result in a CGHG uptake compared to bare peat;
2. CGHG uptake will be greater with maturity of vegetation;
3. greater volumes of *E. angustifolium* will result in greater emission of methane;
4. the presence of *Sphagnum* moss will reduce the magnitude of methane emission; and
5. periods of drought will have a deleterious effect on site CO₂ uptake.

METHODS

Field site

Field trials were conducted on Cadishead Moss (53° 27' 10.8" N, 2° 27' 11.5" W), a UK Site of Biological Importance (SBI) 10 km west-south-west of Manchester, UK (Figure 1) adjacent to peat-extracted Little Woolden Moss. The site is an 8-ha fragment of the once-extensive Chat Moss lowland bog complex which has been mostly urbanised or

drained for agriculture or peat extraction so that only a small fraction of the original complex remains as functioning peatland or under restoration management (Ashby *et al.* 2021). Cadishead Moss was originally ditch-drained and block-cut for peat, then partially abandoned and colonised by trees and scrub until at least 2000, after which some parts (including the trial areas) were mechanically scraped for peat extraction. The Lancashire Wildlife Trust (LWT) acquired the site in 2009, cleared scrub and trees, and rewetted by installing plastic piling and a series of peat bunds, leaving some deep internal ditches remaining. There is now good coverage of *Eriophorum angustifolium* in wetter areas and *Molinia caerulea* in drier areas, with minimal bare peat.

BeadGel™ mix

The commercial BeadaGel™ mix provided by the BeadaMoss® company for our field trials contained eleven *Sphagnum* species in the following proportions: *S. auriculatum* Schimp. (synonym: *S. denticulatum*) ~1 %, *S. capillifolium* (Ehrh.) Hedw. (ssp. *capillifolium*) ~10 %, *S. cuspidatum* Ehrh. Ex Hoffm. ~10 %, *S. fallax* (H. Klinggr.) H. Klinggr. ~25 %, *S. fimbriatum* Wilson ~10 %, *S. medium* Limpr. (likely) (originally designated as *S. magellanicum* Brid.) ~1 %, *S. papillosum* Lindb ~10 %, *S. squarrosum* Crome ~1 %, *S. palustre* L. ~20 %, *S. tenellum* (Brid.) Bory ~1 %, *S. subnitens* Russow & Warnst. ~5 %.

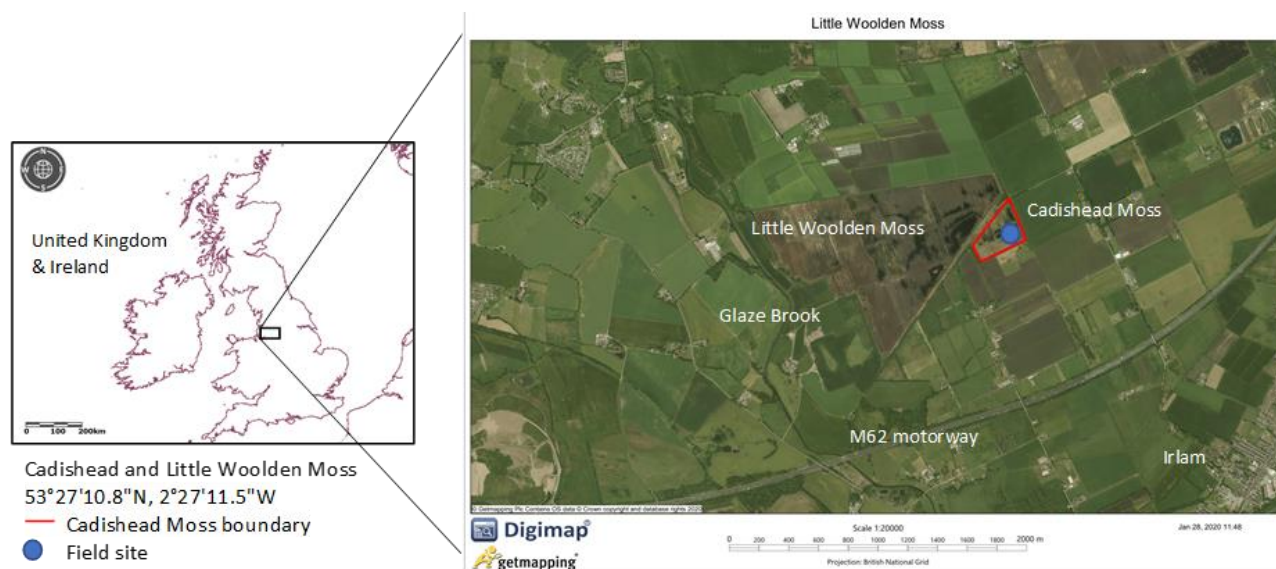


Figure 1. Location map of Cadishead and Little Woolden Mosses, close to the conurbation of Manchester, UK. Cadishead Moss and surrounding landscape matrix: map from EDINA Digimap Ordnance Survey Service <https://digimap.edina.ac.uk/aerial>.

S. magellanicum is now recognised as a species specific to the Southern Hemisphere, and European species similar to *S. magellanicum* are separated into *S. medium* and *S. divinum* (Hassel *et al.* 2018) which have some morphological differences and are generally found, respectively, in ombrotrophic and minerotrophic habitats (Laine *et al.* 2018). The *Sphagnum* sourced for the BeadaMoss® material could be either or a mixture of these, but *S. medium* is assumed. A few strands of each species were

sourced from the Peak District National Park, apart from *S. medium* and *S. tenellum* which were sourced from Cumbria (Caporn *et al.* 2018).

Field plots

Permanent collars were installed in areas of mature and immature *Eriophorum angustifolium*, with and without *Sphagnum*, and bare peat (i.e., five treatments) (Figure 2). All collars were contained within an area of approximately 0.4 ha. Collars were

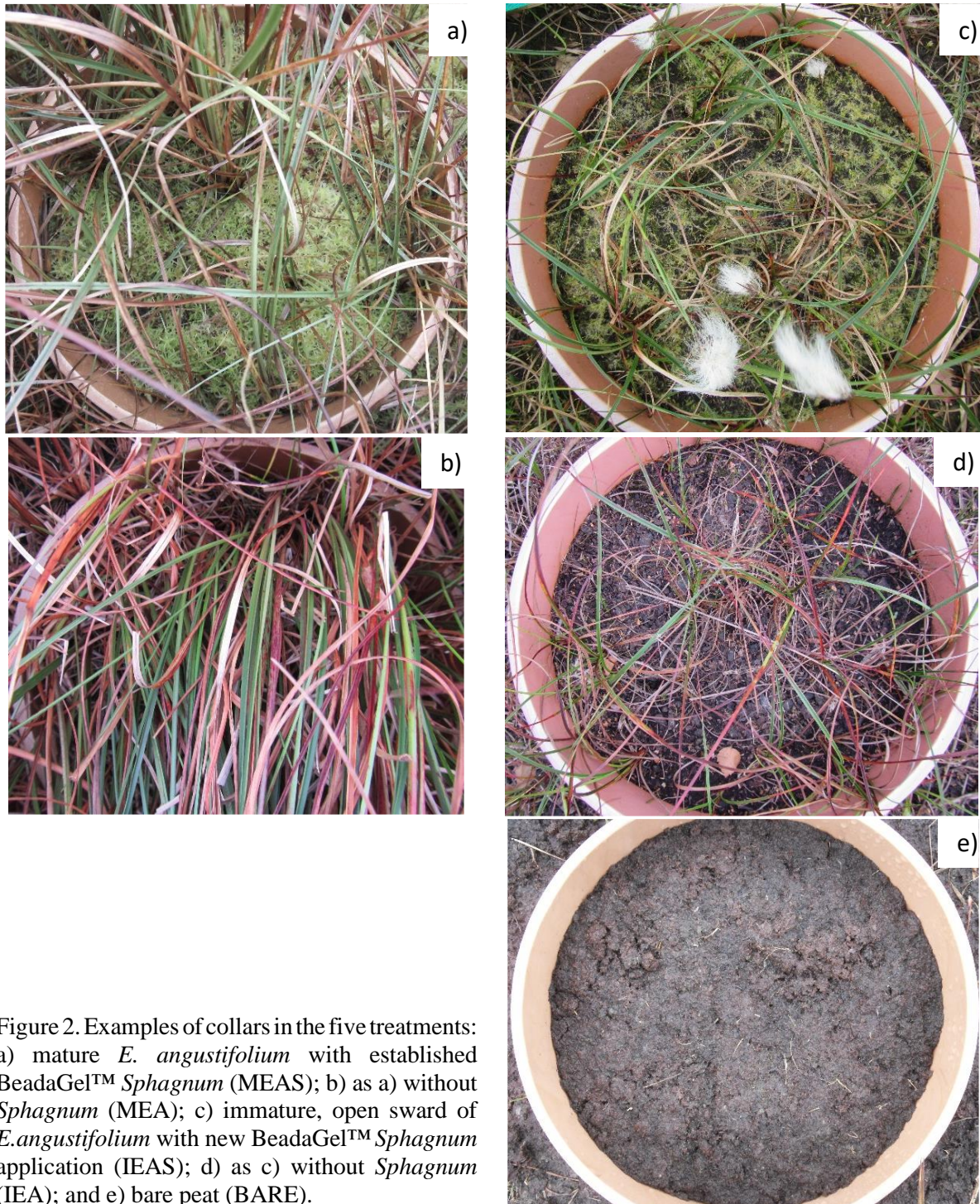


Figure 2. Examples of collars in the five treatments: a) mature *E. angustifolium* with established BeadaGel™ *Sphagnum* (MEAS); b) as a) without *Sphagnum* (MEA); c) immature, open sward of *E.angustifolium* with new BeadaGel™ *Sphagnum* application (IEAS); d) as c) without *Sphagnum* (IEA); and e) bare peat (BARE).

cut from 300 mm internal diameter plastic waste pipe to 100 mm length and eased into the peat, leaving 40–50 mm standing above the surface. The commercial BeadaGel™ mix (see previous sub-section) was applied at a rate of 3 L m⁻² to 1 m² areas with immature, open swards of *Eriophorum angustifolium* (with collars in situ) to allow the gel to reach the peat surface. Preliminary CGHG measurements were made after several months, and regular measurements after one year, so that decomposition of any vegetation and roots damaged by collar placement did not influence the results (Rowson *et al.* 2013).

Six trial ('immature') plots were established in October 2015 in areas of sparse *E. angustifolium* growth. Each plot contained one collar of *E. angustifolium* (IEA), one collar in an area of *E. angustifolium* with new *Sphagnum* BeadaGel™ application (IEAS), and one collar on bare peat (BARE). There were no areas with *Sphagnum* only to provide further controls. At this site, earlier trials of planting *Sphagnum* on bare peat, even with straw mulch, were either not successful or plots were soon colonised by *E. angustifolium*; *Sphagnum* is often only successful in a restoration setting when introduced along with a nurse crop (Quinty & Rochefort 2003, Pouliot *et al.* 2011). BeadaGel™ was slow to establish during the early stages of the trial on 'immature' plots and was reapplied at the same rate six months after the start of GHG measurements, within the collar area only, at which stage removable environmental protection in the form of greenhouse shading mesh was added to simulate straw mulch.

Three further plots (termed 'mature' plots) were set up at the same time on areas established in June 2014 for a previous study, to allow monitoring at a more advanced stage of BeadaGel™ growth in a tall, dense *E. angustifolium* sward. Each 'mature' plot contained two collars within a 1 m² area of *E. angustifolium* plus *Sphagnum* (MEAS) and one collar on *E. angustifolium* without *Sphagnum* (MEA) nearby. There was no bare peat in areas of mature *E. angustifolium*, so bare peat collars are only associated with 'immature' plots. Throughout the trial, any emerging seedlings of vascular plants other than *E. angustifolium* were removed from the experimental plots, and all seedlings were removed from bare plots, to maintain the experimental design.

A plot dipwell was inserted close to each cluster of collars, within 1.5 m of each collar, to monitor water table depth (WTD), and measurements of WTD relative to the peat surface were recorded manually every week when possible, and fortnightly at minimum. Dipwell design followed Allott *et al.* (2009).

Peat cores and peat quality measurements

Peat cores and quality of surface peat within the trial area were examined for insights about the legacy of degradation which may still influence the carbon balance of the site, and what may be done to remedy it. Nine peat cores to 1 m depth were taken with a Russian corer and visually inspected (only).

Before the start of GHG flux field monitoring, three peat samples were collected to 5 cm depth from around each of the trial plots and homogenised to make up one replicate composite sample per plot ($n = 9$). Fresh well-mixed peat samples (5 g of each) were added to 25 ml of deionised (DI) water, stirred regularly, then electrical conductivity was measured (Jenway 4510 analyser) in the order of sample preparation. Samples were re-stirred and pH measured (Jenway 3510 analyser), leaving the probe in the solution for 30 s. Further fresh peat samples were prepared for extraction of ammonium and nitrate using 1% KCl (as recommended by Allen 1989) for ion chromatography (IC) (Thermo Scientific Dionex AS analyser) and extraction of elements (Ca, Fe, K, Mg and P) using 0.1M EDTA (as recommended by Lo & Yang 1999) for inductively coupled plasma - optical emission spectrometry (ICP-OES) (Thermo Scientific iCAP 6000 Series ICP Spectrometer). Extractable values were seen as more useful determinants of element bioavailability in the peat than total values (Rosenburgh 2015). Peat samples (mean mass 2.5316 ± 0.0235 g) were put into 100 ml conical flasks, including one blank sample for each extraction, with 25 ml of the appropriate extraction solution, and the flasks were agitated on an orbital shaker for 30 minutes. Samples were filtered through Sartorius™ Minisart™ Plus Syringe Filters (0.2 µm) into tubes for analysis (1 ml for IC and a minimum of 10 ml for ICP-OES), discarding the first 5 ml of filtrate to remove any filter contaminants.

The remainder of the fresh samples were weighed, then oven dried overnight at 105 °C and weighed again to find the mass difference to give sample moisture content. Samples were removed for dry analysis and the remainder re-weighed and placed in a muffle furnace at 550 °C for three hours to find the mass difference (loss-on-ignition) from which organic matter and mineral fractions were estimated. Total C and N content were analysed (LECO FP628 elemental analyser) using 0.1513 ± 0.0006 g (mean sample mass) of dry, ground peat placed into tared aluminium foil cups twisted into capsules, with five calibration capsules prepared in the same way using EDTA LECO calibration 502-092 (mean mass 0.1508 ± 0.0005 g).

Gas flux and environmental monitoring

CGHG measurements were obtained using a Los Gatos Research™ (LGR) ‘Ultraportable Greenhouse Gas Analyser (CH₄, CO₂, H₂O)’ (manufactured by Los Gatos Research, San Jose, California, USA), which has < 2 ppb precision for CH₄ and < 300 ppb precision for CO₂ at a 1 second measurement rate. A closed chamber system was created using a clear (Perspex) chamber whereby changes in gas uptake or emission due to plant and soil photosynthesis and respiration could be measured in real time. A Perspex extension was used for taller vegetation, with a partially inflated rubber tyre attached to create a good seal between the collar and the chamber and extension, similar to methods used on automated chambers at Mer Bleue bog (Lai *et al.* 2012). Gases were directed around the chamber via a ring of tubing, pierced at 1 cm intervals and blocked with silicone gel half-way along to prevent gas cycling in the tube. Each end of the tubing ring was attached via more tubing through the chamber to the inlet and outlet ports of the LGR analyser. A small (9V) fan inside the chamber ensured good gas circulation (tested prior to use). The gas temperature was continuously recorded by the LGR analyser.

CGHG fluxes from each collar were recorded fortnightly during the growing season and monthly during winter for two full years from September 2016 to August 2018, i.e. there were 33 monitoring visits. All collars were monitored, in random order, during each visit. Photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$), peat temperature at 5 cm depth and WTD were recorded during measurements, as recommended by Alm *et al.* (2007). A soil temperature probe (Delta-T Devices Ltd) and PAR meter (Skye Instruments Ltd) were attached to a GP1 Delta-T logger, recording measurements at 10 s intervals.

Dark and light measurements were each taken over a 2-minute period (Davidson *et al.* 2016) with the chamber firstly obscured with a blackout cloth, then aerated before a measurement with the chamber uncovered, to obtain measurements of net ecosystem respiration (NER), net ecosystem exchange (NEE) and CH₄ flux.

Volume of vegetation and headspace within collars

The volumes of the Perspex chamber and extension were known constants. The volume of headspace within the collar was variable owing to changes in the volume of vegetation and swelling/shrinkage of the peat. The depth from top of collar to peat or *Sphagnum* surface was measured at six internal peripheral positions after each gas measurement, and the headspace volume within the collar calculated

and added to the chamber/extension volume for flux calculations. If the *Sphagnum* surface was above the top of the collar, its distance from the collar top was measured after each gas measurement at four internal peripheral positions (midway between centre and edge of collar) and at the highest point (usually central) to obtain a mean height above the collar, giving a negative collar headspace volume.

The volume of *E. angustifolium* within collars was calculated from monthly measurements of the number and length of plants (longest leaf; as outlined by Davidson *et al.* 2016). If there was dense growth (i.e., more than about 40 plants), the plants were counted and 10 % of representative plants at random peripheral and central positions were measured to obtain a mean. Seasonally, *E. angustifolium* plants from the site (not within collars) were cut, measured (longest leaf), and the volume of each plant determined by water displacement. Separate scatter graphs of length against volume were plotted for non-flowering and flowering/seeding plants, and used in calculating the volume of plants in each collar (spring, autumn and winter $R^2 = 0.7\text{--}0.8$; summer $R^2 = 0.54$ (non-flowering) to 0.6 (flowering)). The volume of *E. angustifolium* (assessed monthly) was subtracted from the headspace when calculating CGHG fluxes.

Measurements of *E. angustifolium* and *Sphagnum* volumes were also used to assess above-ground plant competition and any influence of the changing volume of vegetation on CGHG fluxes over time. Thickness of the *Sphagnum* layer within a collar was estimated as the mean of measurements obtained at nine positions by probing to the recolonised peat surface (which was firm) with a narrow, blunt-ended rod. *Sphagnum* volume was then calculated as that of a cylinder with this height and basal area derived from the estimated percentage *Sphagnum* cover within the collar. Care was taken to minimise damage to the *Sphagnum* when taking measurements.

CGHG measured flux data management

CO₂ and CH₄ measurements were downloaded from the LGR into Excel spreadsheets and fitted to an Excel linear regression model to obtain gradient (slope), R^2 and p -values for each 2-minute measurement. Graphs were used to visualise and remove erroneous start or end measurements, as recommended by Evans *et al.* (2016). The maximum number of observations retained per measurement was 124 and the minimum number was 60. Erroneous periods of measurement could be due to test error or, particularly in summer light levels, low CO₂ availability in the chamber due to high uptake by plants, causing a reduction in slope. Regression line

thresholds of $R^2 > 0.7$ and $p < 0.05$ were applied to screen for acceptable measurements, similar to protocols used by Evans *et al.* (2016). If neither of these conditions was met the measurement was discarded, but as CO₂ and CH₄ gases were measured concurrently, if one measurement met the criteria a system integrity failure was deemed unlikely and both gas measurements were retained. Only 1 % of all flux measurements were discarded.

Fluxes (g m⁻² h⁻¹) were calculated separately for CO₂ and CH₄ using an equation adapted from Dossa *et al.* (2015):

$$\text{Flux} = (\Delta\text{CO}_2/t) * (PV/RT) * (1/A_s) * ((44*60*60)/1000) \quad [1]$$

where P (atm) is atmospheric pressure, V (m³) is chamber volume, R (L atm mol⁻¹ K) is the universal gas constant, T (K) is gas temperature, A_s (m²) is surface area within the collar, and 44 (g mol⁻¹) is the molecular weight of CO₂ (substituted with 16 g mol⁻¹ for CH₄ calculations).

Measurements from the dark and light chambers gave Net Ecosystem Respiration (NER) and Net Ecosystem Exchange (NEE), respectively. Gross Primary Productivity (GPP) was calculated as:

$$GPP = NEE - NER \quad [2]$$

and values used for further analysis of flux data.

The micrometeorological sign convention was adopted, whereby negative fluxes indicate removal from the atmosphere and positive fluxes indicate addition to the atmosphere.

Methane fluxes were calculated from measurements in the dark. CO₂ equivalents of CH₄ were calculated as $GWP_{100} \times 28$ (Myhre *et al.* 2013) as adopted in the 1997 Kyoto Protocol, when calculating CGHG budgets as CO₂e in g m⁻² yr⁻¹.

Statistical analysis of measured data

Measured vegetation and flux data from all treatment groups (MEAS, MEA, IEAS, IEA, BARE; see Figure 2) were tested for normality using Shapiro Wilk tests, and were found to be not normally distributed. A non-parametric test for repeated measurements (Friedman's test) was used to determine any statistically significant difference between groups and post hoc analysis of flux data with Wilcoxon signed-rank tests was conducted with a Bonferroni correction applied, resulting in a significance level set at $p < 0.0083$ throughout. Data were analysed statistically using IBM SPSS Statistics for Windows (Version 25.0. Armonk, NY: IBM Corp.) and through the data analysis tools in Microsoft Excel (2019).

CGHG flux data modelling

Hourly air temperature (°C), rainfall (mm) and total solar radiation (W m⁻²) datasets for the full period of measurement (01 Sep 2016 to 31 Aug 2018) were provided by the Whitworth Meteorological Observatory (CAS 2020) at the University of Manchester, 14.8 km east-north-east of the study site. Photosynthetically Active Radiation (PAR) (μmol m⁻² s⁻¹) was derived from solar radiation (W m⁻²) assuming PAR (400–700 nm) is 45 % of total solar radiation, using the conversion factor $1 \text{ W m}^{-2} \approx 2.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Biggs 1984).

A linear regression between peat temperature (PT) and air temperature (AT) measurements from micrometeorological equipment on the neighbouring Little Woollen Moss (LWM; Figure 1) was applied to the Whitworth Observatory AT data to provide integrated PT data for the period of CGHG measurements. The record for WTD, measured weekly to fortnightly throughout the study period, was infilled assuming linear changes between measurements, to provide an estimated hourly dataset (Alm *et al.* 2007, Renou-Wilson *et al.* 2019).

The measured CGHG flux data were plotted against the measured environmental variables PT, WTD and PAR and the linear regression R^2 values were ranked to determine which variables best explained the measured values of NER, GPP and methane fluxes (i.e., primary, secondary and tertiary drivers). GPP values were made positive for ease of data manipulation, then non-linear regression (usually exponential) equations were fitted between each measured flux and primary driver to create each primary model. For y_1 , exponential regression ($f: x_1$):

$$y_1 = abx_1 \quad [3]$$

where a = coefficient (or y-intercept), b = exponent and x_1 = one of the independent environmental variables, i.e. PT (°C) or WTD (cm) or PAR (μmol m⁻² s⁻¹). A linear regression may have interpolated the data better, but an exponential equation ensured that no abnormal negative flux values were introduced. Data from this model were subtracted from measured flux data, to leave residual data. Linear regression equations from residual data were fitted with the secondary driver (and subsequently with the tertiary driver, where used); e.g. for y_2 linear regression (residual: x_2)

$$y_2 = mx_2 + c \quad [4]$$

(where m = line gradient and c = co-efficient, or y-intercept). These equations were added iteratively to the primary model, checking for goodness of fit with measured flux data at each stage, to create a final model:

$$f_m = abx_1 + [(f - abx_1)x_2 + c] \quad [5]$$

where f and f_m = measured and modelled fluxes in CO₂e (g m⁻² h⁻¹).

Equations 3 and 4 were applied to hourly environmental data to provide an integrated model for gaseous fluxes for each treatment. Modelled values for GPP were adjusted to zero when PAR was zero. NEE was calculated from NER and GPP (Equation 2). All data were manipulated using data analysis tools in Microsoft Excel (2019).

The amalgamated treatment data were also modelled using a range of other equations from literature, to check the validity of our model. NER was modelled using a Lloyd & Taylor (1994) model, which is based upon an Arrhenius equation, adapted to incorporate both PT and WTD. NER was also modelled using an extension of that model, developed by Rowson *et al.* (2013), which is a peat temperature model but incorporates a range of environmental variables, as described by Creevy *et al.* (2020). GPP was modelled using equations which all rely on the relationship between GPP and PAR: ($\alpha * GP_{max} * PAR$)/($\alpha * PAR + GP_{max}$) (Michaelis & Menten 1913); ($\alpha * PAR$)/(1 - (PAR/2000) + ($\alpha * PAR/GP_{max}$)) (Falge *et al.* 2001); and: ($\alpha * PAR * GP_{max}$)/sqrt($GP_{max}^2 + (\alpha * PAR)^2$) (Smith (1936). The alpha constants were derived using Microsoft Excel Solver.

An annual CGHG flux value for each treatment was calculated from the sum of hourly values for each modelled flux dataset for each full year of study (September to August). CO₂ equivalents of CH₄ were calculated by multiplying methane values by a Global Warming Potential (GWP)₁₀₀ of 28 and adding to NEE (balance of NER and GPP), to give a CGHG budget in CO₂e (g m⁻² yr⁻¹). Datasets were analysed for normality using PAST software and found to be not normally distributed through Shapiro-Wilk tests (cross-referenced with Jarque-Bera tests due to large datasets: $n = 8760$). Differences in fluxes between years within treatment groups were analysed using Microsoft Data Analysis two-sample tests assuming unequal variances. Differences in CGHG flux between treatment groups for each year were tested using PAST software (Kruskal-Wallis with post-hoc Mann-Whitney pairwise test).

RESULTS

Water table depth and meteorological data

Despite higher-than-average rainfall in the preceding three seasons, low rainfall during May to August of Year 2 resulted in a prolonged drought accompanied

by a dramatic summer drop in water table to -48 ± 5.9 and -54 ± 6.9 cm (lowest mean value, relative to ground surface) in mature and immature plots respectively, which was 2.1 and 1.7 times (respectively) the largest WTDs recorded during the summer of Year 1 (Figure 3). Long-term average (LTA) data for the area, sourced from the UK Met Office, showed that rainfall was more variable in Year 2 than in Year 1, and in both years was generally higher than average in cooler months and lower than average in warmer months.

Vegetation data

In both years, the volume of *E. angustifolium* in MEAS and IEAS collars (Mature and Immature *E. angustifolium* with *Sphagnum*, respectively) increased rapidly from April and reduced from October, with greater proportional increase in growth in IEAS than MEAS plots. *Sphagnum* volume in both MEAS and IEAS plots levelled off from October/November each year. During the growing season, *Sphagnum* volume increased in MEAS collars in Year 1 but gradually decreased in Year 2, whereas in IEAS collars, *Sphagnum* volume increased throughout, although at a reduced rate during the Year 2 summer drought.

The volume of *E. angustifolium* in both MEA and IEA collars (Mature and Immature *E. angustifolium*-only, respectively) changed similarly over the study period, increasing from April and reducing from October (more quickly in IEA collars), but levelled off during the Year 2 Summer drought (reducing slightly in IEA collars).

There was a statistically significant difference in the volume of *E. angustifolium* between MEAS and MEA plots: $\chi^2(2) = 16.860$, $p < 0.001$, $df = 1$ as determined by a Friedman Test, (MEA > MEAS). Moreover, in MEAS plots, *E. angustifolium* volume reduced slightly in Year 2, whereas in MEA plots it increased by 23.5 %. There was a statistically significant difference in the volume of *E. angustifolium* between IEAS and IEA plots: $\chi^2(2) = 20.211$, $p < 0.001$, $df = 1$ as determined by a Friedman Test, with an increasingly greater volume in IEAS than in IEA plots; by 21.2 % in Year 1 and by 42.3 % in Year 2.

Sphagnum volume (zero values in IEAS Year 1 removed) increased overall from Year 1 to Year 2, in MEAS plots by 37.8 % and in IEAS plots by 314 %. However, during the Year 2 summer drought there was obvious drying of vegetation. *Sphagnum* became bleached and the action of taking measurements on collars containing mature *Sphagnum* (which had grown above the top of the collar) isolated plants within the collar from the surrounding *Sphagnum*

carpet. This created a dry edge effect which was less pronounced in collars of immature vegetation, where *Sphagnum* was shorter than the collar and benefitted from mesh shading. Peat shrank in BARE treatments and in some collars of immature *E. angustifolium*, creating a gap between peat and collar.

Peat cores and peat surface samples analysis

Peat cores were visibly different in terms of peat colour, texture and plant species content but had dark and coarse or open-textured (oxidised) peat at the surface, to a depth of 10–28 cm, containing coarse stems and roots of *E. angustifolium*. In most cores there was friable peat at the surface, to a depth of 3–24 cm. Peat colour then changed to variously striated mixtures of black/orange with varying openness of texture, and fine *E. angustifolium* roots throughout. The surface peat characteristics appear typical for a lowland bog (Table 1) although NO_3 and NH_4 levels were high.

Measured flux data

The closed chamber system with the Los Gatos analyser delivered accurate results (94 % above the 0.7 R^2 threshold criteria), with very few (1 %) discarded measurements (Table 2). Reporting of flux

measurements is by replicates of chamber measurements for each treatment across the study period or for each study year (September to August). Measured fluxes of CO_2 and CH_4 (Figure 4) followed the seasonal pattern of rising towards higher summer temperatures and plant and microbial activity, and falling towards lower winter temperatures, plant senescence and reduced microbial activity.

All fluxes from mature vegetation were greater ($p < 0.001$ throughout) and more variable than those from immature vegetation (mature vegetation: NER 0.018 to 1.031 and GPP -0.019 to -1.91 $\text{g m}^{-2} \text{h}^{-1}$; CH_4 0.3 to 2.7 $\text{mg m}^{-2} \text{h}^{-1}$; immature vegetation: NER 0.014 to 0.51 and GPP -0.020 to -0.87 $\text{g m}^{-2} \text{h}^{-1}$; CH_4 0.4 to 1.2 $\text{mg m}^{-2} \text{h}^{-1}$), and the large range in flux values from each collar can clearly be seen in Figure 4. In mature vegetation, uptake of CO_2 , respiration and CH_4 emissions were greater in plots without *Sphagnum*, which had greater abundance of vascular plants. In immature vegetation, respiration and CH_4 emissions were similar, but uptake of CO_2 was greater in plots with *Sphagnum* (which had lower abundance of vascular plants). NER and CH_4 emissions were greater in vegetated plots than bare plots, but there was an overall CO_2 uptake on vegetated plots. Bare plots had some GPP (mean (SE):

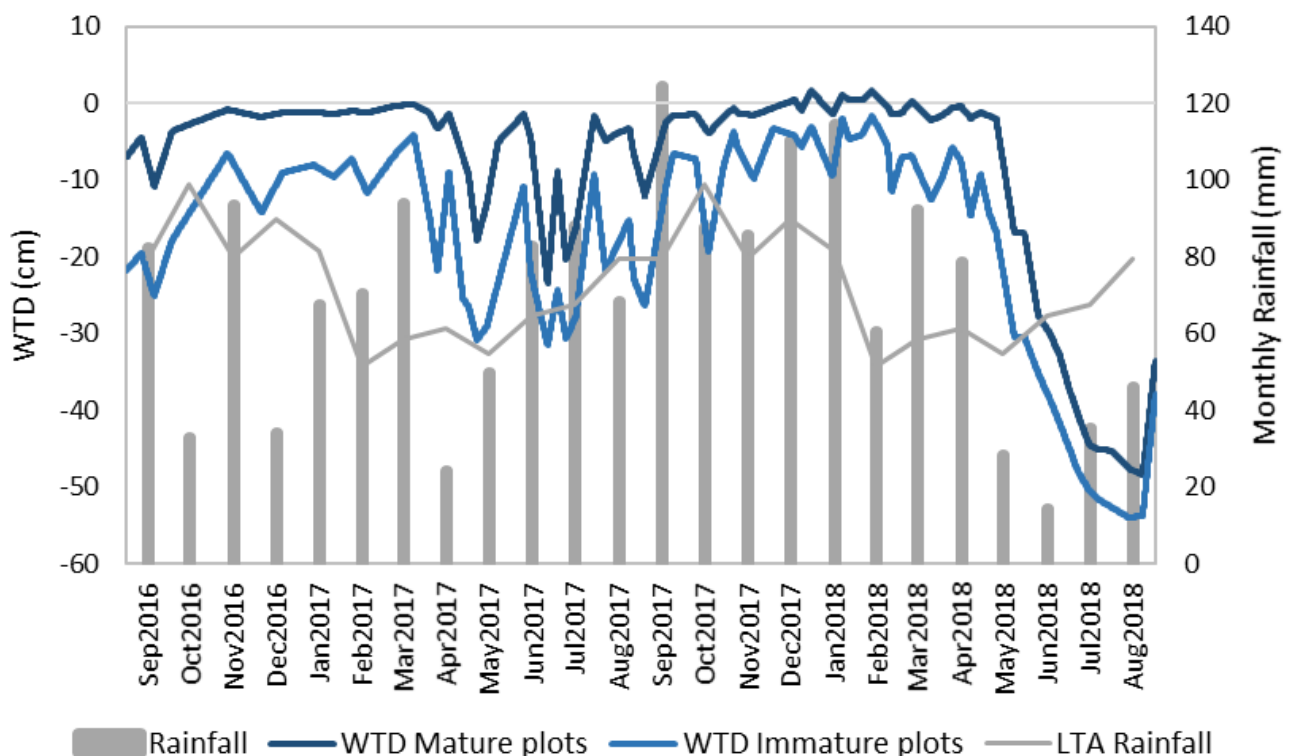


Figure 3. Monthly rainfall, long term average (LTA) rainfall, and corresponding mean water table depth (WTD) below the surface, measured across treatment plots grouped by vegetation maturity; study period September 2016 to end-August 2018. LTA (1981 to 2010) rainfall (monthly mean) from Woodford Meteorological Station (53° 20' 24.0" N, 2° 09' 14.4" W), 20 km south-east of the site.

(SE): -0.05 (0.004) g m⁻² h⁻¹) due to algal growth and patches of acrocarpous mosses, but NER was the strongest flux, resulting in CO₂ emission for much of the study period. Methane fluxes were low

throughout, with mean (SE) values of 1.01 (0.05) mg m⁻² h⁻¹ for Mature vegetation, 0.80 (0.02) mg m⁻² h⁻¹ for Immature vegetation, and 0.12 (0.008) mg m⁻² h⁻¹ for BARE.

Table 1. Site characteristics and surface peat properties. Climate data (Met Office 2023) are ten-year (1991–2020) average values from Woodford Observing Site (53° 20' 24.0" N, 2° 09' 14.4" W; 88 m a.s.l.), 23 km SE of Cadishead Moss. Study period 01 Sep 2016 to 31 Aug 2018. Peat properties: mean values ($n = 9$). Total C and N analysed on LECO Element analyser; EDTA extractable P, K, Ca, Mg analysed on ICP-OES after acid digest with 0.1M EDTA; nitrate and ammonium analysed on KCl-extract using Dionex ion chromatography. Concentrations are on a dry weight basis.

Site characteristics		Peat properties			
Site area	8 ha	NH ₄ ⁺ (mg kg ⁻¹)	3.55±3.41	pH	4.86±0.21
Elevation	23 m a.s.l.	NO ₃ ⁻ (mg kg ⁻¹)	1.72±4.34	EC (µS m ²)	45.46±4.54
Average rainfall	868 mm yr ⁻¹	P (mg g ⁻¹)	0.001±0.001	%Moisture	86±3
Mean annual air temp	9.8 °C	K (mg g ⁻¹)	0.016±0.018	%OM	96±2
Mean Jan air temp	4.1 °C	Ca (mg g ⁻¹)	3.31±0.81	%N	1.41±0.08
Mean Jul air temp	16.2 °C	Mg (mg g ⁻¹)	0.55±0.38	%C	50.81±0.95
Peat depth	2.3±0.3 m	Bulk density (g cm ⁻³)	0.097±0.023	C/N	36.12±2.36

Table 2. Results of statistical tests between treatment groups for measured flux values. Friedman's test (X^2 , df , sample no.) and post-hoc (Wilcoxon signed-rank tests Z) tests with statistical significance $p < 0.0083$. NER = Net Ecosystem Respiration, GPP = Gross Primary Productivity, NEE = Net Ecosystem Exchange. Treatments: M = Mature, I = Immature; EA = *E. angustifolium*-only; EAS = *E. angustifolium* with *Sphagnum*. NS = no statistical significance.

Measured flux		NER	GPP	NEE	methane
All treatments	X^2 (4, $n = 99$)	287.141	257.130	167.064	223.055
	p	< 0.001	< 0.001	< 0.001	< 0.001
MEA : MEAS	Z	-6.949	-6.070	-4.904	-2.841
	p	< 0.001	< 0.001	< 0.001	0.004
IEA : IEAS	Z	NS	-5.993	-5.993	NS
	p		< 0.001	< 0.001	
MEAS : BARE	Z	-11.633	-12.178	-11.785	-12.091
	p	< 0.001	< 0.001	< 0.001	< 0.001
MEA : BARE	Z	-8.638	-8.628	-8.195	-8.638
	p	< 0.001	< 0.001	< 0.001	< 0.001
IEAS : BARE	Z	-11.002	-12.050	-11.889	-12.194
	p	< 0.001	< 0.001	< 0.001	< 0.001
IEA : BARE	Z	-11.329	-11.785	-11.243	-12.063
	p	< 0.001	< 0.001	< 0.001	< 0.001

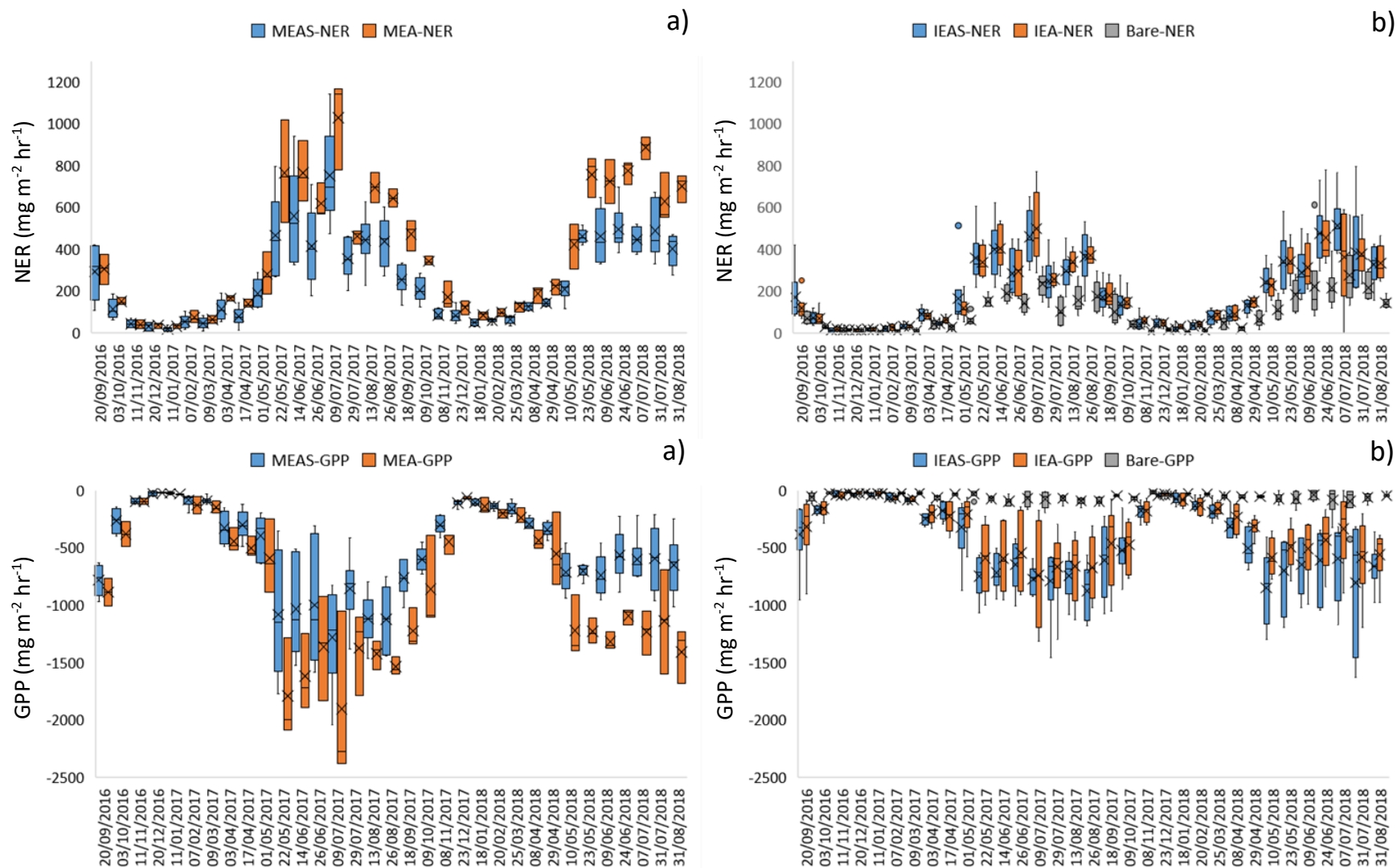


Figure 4. Measured Net Ecosystem Respiration (NER) (above) and Gross Primary Productivity (GPP) (below) flux values for each measurement visit (dates are shown on the horizontal axis) in (a) mature and (b) immature plots. MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*); MEA = mature vegetation (*E. angustifolium* only); IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*); IEA = immature vegetation (*E. angustifolium* only); BARE = bare peat. In box plots, crosses indicate the mean value, lines indicate the median, and interquartile range is exclusive.



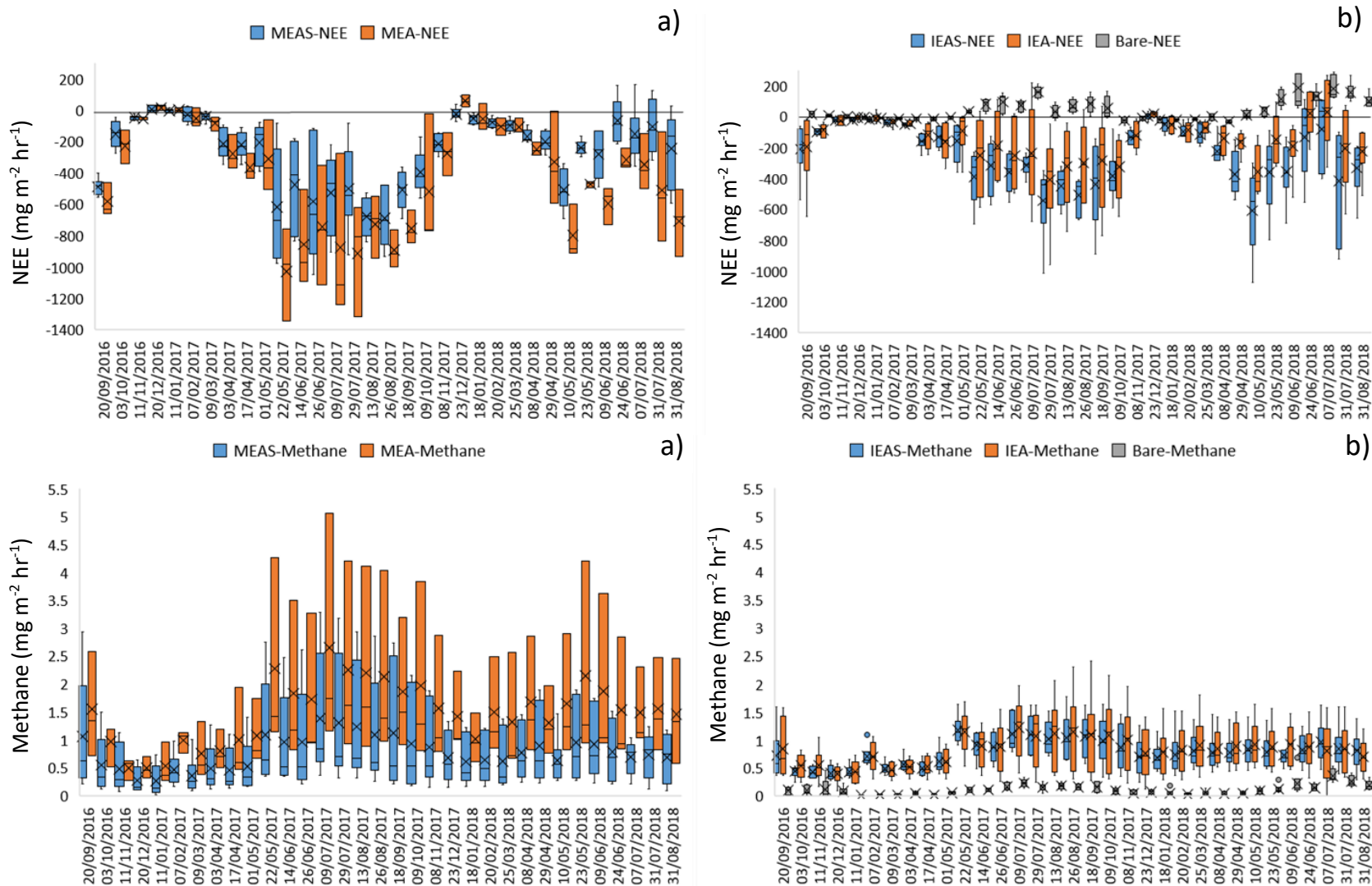


Figure 4 (continued). Measured Net Ecosystem Exchange (NEE) (above) and methane (below) flux values for each measurement visit (dates are shown on the horizontal axis) in (a) mature and (b) immature plots. MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*); MEA = mature vegetation (*E. angustifolium* only); IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*); IEA = immature vegetation (*E. angustifolium* only); BARE = bare peat. In box plots, crosses indicate the mean value, lines indicate the median, and interquartile range is exclusive.



Measured flux data and environmental variables

Relationships between the primary driver peat temperature at 5 cm depth (PT) and the secondary driver water table depth (WTD) appeared to explain most of the variability in NER and methane fluxes, and PT followed by PAR then WTD explained variability in GPP (Table 3). GPP appeared to increase until the peat temperature was 16–17 °C, then reduce above this temperature, particularly in immature vegetation where PT was notably higher (maximum 23.5 °C) than in plots with mature vegetation (maximum 19.3 °C). Methane flux increased with greater volumes of *E. angustifolium* ($R^2 = 0.2553$ for Mature, 0.3838 for Immature) but there was no apparent relationship between volume of *Sphagnum* and magnitude of any flux.

Modelled flux data

Modelling of data by treatment, using our model and a range of other models from the literature, produced higher NER R^2 and lower SSE values for the Rowson *et al.* (2013) model in comparison with our own and Lloyd & Taylor + WTD models (Table 4). In contrast, GPP R^2 and SSE values for literature models (Michaelis-Menten, Falge, Smith) were generally poorer than for our model. Annual NER flux values derived from our model and Rowson *et al.* (2013) were very similar, and lower than the fluxes predicted by Lloyd & Taylor + WTD (Table 5). However, for annual GPP flux results, our model generally produced higher values than literature models (although not for BARE treatment) but graphs of modelled and measured fluxes showed a better and

Table 3. R^2 values, coefficients (Standard Error) of linear regression to test relationships between measured environmental variables and fluxes prior to modelling data. MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*); MEA = mature vegetation (*E. angustifolium* only); IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*); IEA = immature vegetation (*E. angustifolium* only); BARE = bare peat; NER = net ecosystem respiration; GPP = gross primary productivity; NEE = net ecosystem exchange; PT = peat temperature (°C); WTD = water table depth (cm); PAR = photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Reported as collated collar values for each treatment. (Data points = 199 other than MEA = 100.)

		MEAS	MEA	IEAS	IEA	BARE		
NER	PT	R^2	0.6418	0.7210	0.5853	0.5822	0.5331	
		Coeff (SE)	0.0406 (0.0022)	0.0609 (0.0038)	0.0261 (0.0016)	0.0241 (0.0015)	0.0130 (0.0009)	
	WTD	R^2	0.3428	0.4450	0.4087	0.4644	0.4921	
		Coeff (SE)	0.0097 (0.0009)	0.0157 (0.0018)	0.0082 (0.0007)	0.0082 (0.0006)	0.0050 (0.0004)	
	GPP	PT	R^2	0.5206	0.6632	0.4524	0.3102	0.1021
			Coeff (SE)	-0.0715 (0.0049)	-0.1171 (0.0085)	-0.0453 (0.0036)	-0.0326 (0.0035)	-0.0029 (0.0006)
PAR		R^2	0.2923	0.3179	0.2989	0.2534	0.1081	
		Coeff (SE)	-0.0004 (4.97E-05)	-0.0007 (9.96E-05)	-0.0003 (3.82E-05)	-0.0003 (3.50E-05)	-3.08E-05 (6.33E-06)	
WTD		R^2	0.0889	0.2176	0.1961	0.1378	0.0645	
		Coeff (SE)	-0.0097 (0.0022)	-0.0220 (0.0042)	-0.0112 (0.0016)	-0.0083 (0.0015)	-0.0009 (0.0002)	
METHANE (as CO ₂ e)	PT	R^2	0.0694	0.1130	0.1323	0.0406	0.3181	
		Coeff (SE)	0.0013 (0.0003)	0.0024 (0.0007)	0.0007 (0.0001)	0.0005 (0.0002)	0.0003 (3.17E-05)	
	WTD	R^2	0.0000	0.0026	0.0116	0.0113	0.3295	
		Coeff (SE)	-3.97E-06 (1.11E-04)	0.0001 (0.0002)	7.61E-05 (5.03E-05)	9.80E-05 (6.58E-05)	0.0001 (1.25E-05)	

consistent fit for our GPP model compared to those from literature (Figures A1–A4 in the Appendix).

Modelled and measured values (Figure 5) showed similar trends although modelled GPP had high extrapolated points during peak-temperature periods, particularly in Mature vegetation treatments. In Year 1, Modelled winter flux values appeared to be greater

than measured values, although the values were small, but generally the remainder of the measured fluxes were within the range of modelled values. There was high variability in measured values of methane fluxes, which the model smoothed to follow the measured mean, although modelled winter values were a little higher than measured values in Year 1.

Table 4. Comparison of R^2 (SSE: sum of squared estimate of errors) values obtained for linear regressions between measured and variously modelled data for NER and GPP by treatment groups. MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*), MEA = mature vegetation (*E. angustifolium* only), IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*), IEA = immature vegetation (*E. angustifolium* only) and BARE = bare peat control plots.

R ² values (SSE)	NER			GPP			
	This Study	Lloyd & Taylor (1994) + WTD	Rowson <i>et al.</i> (2013)	This Study	Michaelis & Menten (1913)	Falge <i>et al.</i> (2001)	Smith (1936)
MEAS	0.55 (4.55)	0.65 (4.03)	0.72 (2.58)	0.47 (19.33)	0.30 (24.68)	0.30 (24.67)	0.30 (24.71)
MEA	0.61 (4.46)	0.73 (3.40)	0.82 (1.64)	0.48 (24.74)	0.33 (25.14)	0.33 (38.79)	0.32 (25.33)
IEAS	0.46 (4.08)	0.59 (2.69)	0.65 (2.22)	0.29 (19.77)	0.33 (16.79)	0.32 (17.00)	0.32 (50.30)
IEA	0.45 (3.68)	0.59 (2.43)	0.67 (1.97)	0.23 (14.91)	0.28 (13.37)	0.28 (13.37)	0.28 (13.32)
BARE	0.38 (1.61)	0.57 (0.83)	0.61 (0.75)	0.18 (0.38)	0.12 (2.20)	0.12 (2.26)	0.12 (5.05)

Table 5. Comparison of annual CO₂ flux values (g m⁻² yr⁻¹) obtained through variously modelled data for NER and GPP by treatment groups (all collar data within each group). MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*), MEA = mature vegetation (*E. angustifolium* only), IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*), IEA = immature vegetation (*E. angustifolium* only) and BARE = bare peat control plots.

Annual modelled flux comparisons		NER			GPP			
		This Study	Lloyd & Taylor (1994) + WTD	Rowson <i>et al.</i> (2013)	This Study	Michaelis & Menten (1913)	Falge <i>et al.</i> (2001)	Smith (1936)
MEAS	Year 1	2082.34	2457.44	2067.44	-2622.53	-1359.65	-1347.09	-1315.20
	Year 2	2067.68	2449.82	2065.86	-2231.26	-1431.94	-1420.70	-1389.69
MEA	Year 1	3190.40	3448.65	3169.61	-4107.46	-2068.49	-1226.75	-1982.67
	Year 2	3191.75	3461.93	3165.34	-3644.63	-2178.29	-1288.91	-2097.31
IEAS	Year 1	1055.66	1431.60	1207.14	-1570.75	-1195.43	-1226.75	-1982.67
	Year 2	1071.74	1524.63	1237.25	-1495.38	-1244.09	-1288.91	-2097.31
IEA	Year 1	1097.26	1403.56	1192.52	-1237.02	-956.60	-956.60	-922.03
	Year 2	1121.77	1479.55	1216.15	-1192.39	-998.45	-998.45	-964.86
BARE	Year 1	451.74	639.18	531.08	-198.69	-364.49	-367.50	-478.70
	Year 2	460.17	710.10	587.54	-203.94	-382.36	-385.70	-505.68

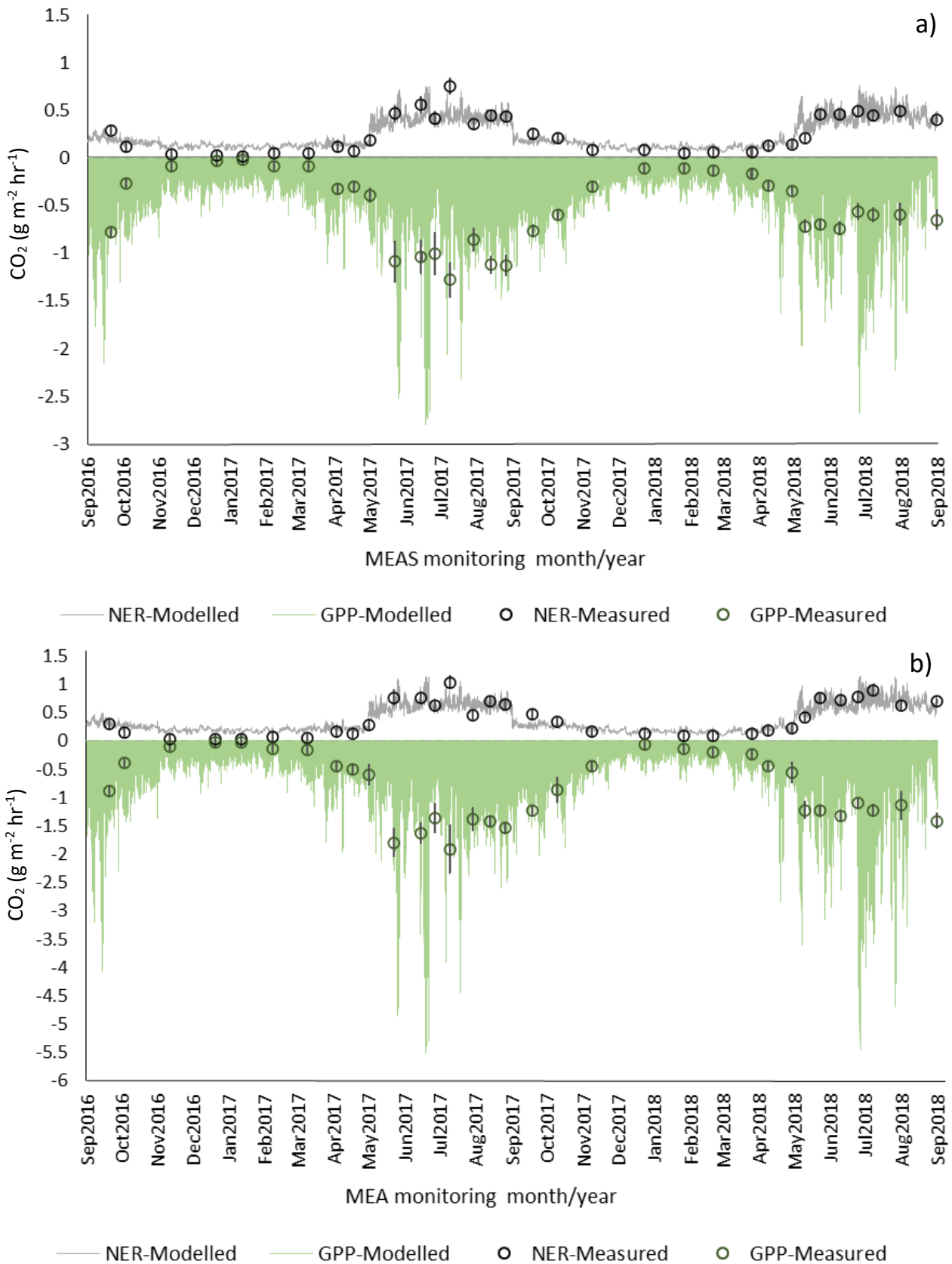


Figure 5. Modelled and measured Net Ecosystem Respiration (NER) (Rowson *et al.* 2013 model) and Gross Primary Productivity (GPP) (This Study model) on treatments a) MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*), b) MEA = mature vegetation (*E. angustifolium* only), Lines show modelled hourly data, points show mean measurements \pm SE.

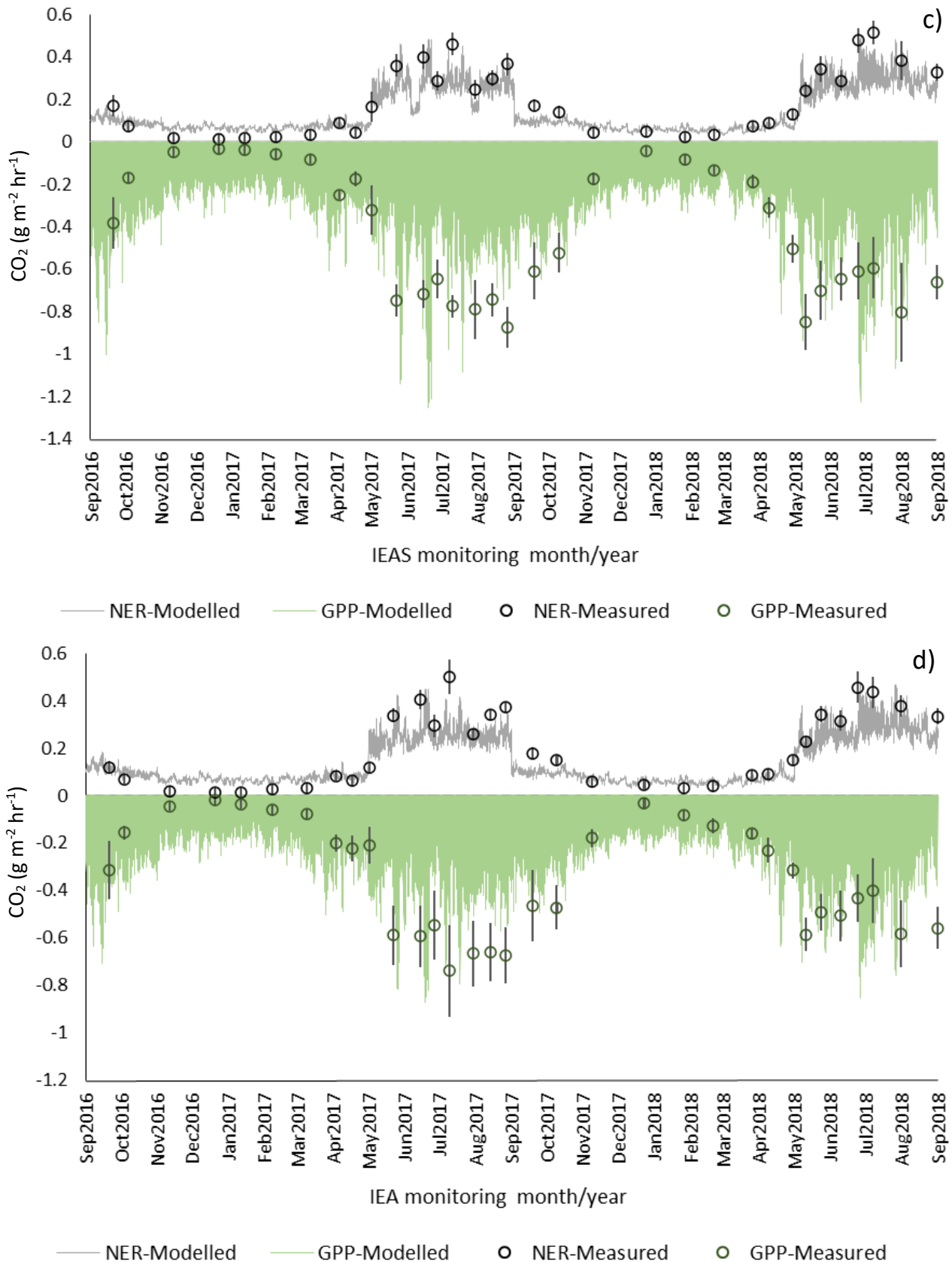


Figure 5 (continued). Modelled and measured Net Ecosystem Respiration (NER) (Rowson *et al.* 2013 model) and Gross Primary Productivity (GPP) (This Study model) on treatments c) IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*), d) IEA = immature vegetation (*E. angustifolium* only), Lines show modelled hourly data, points show mean measurements \pm SE.

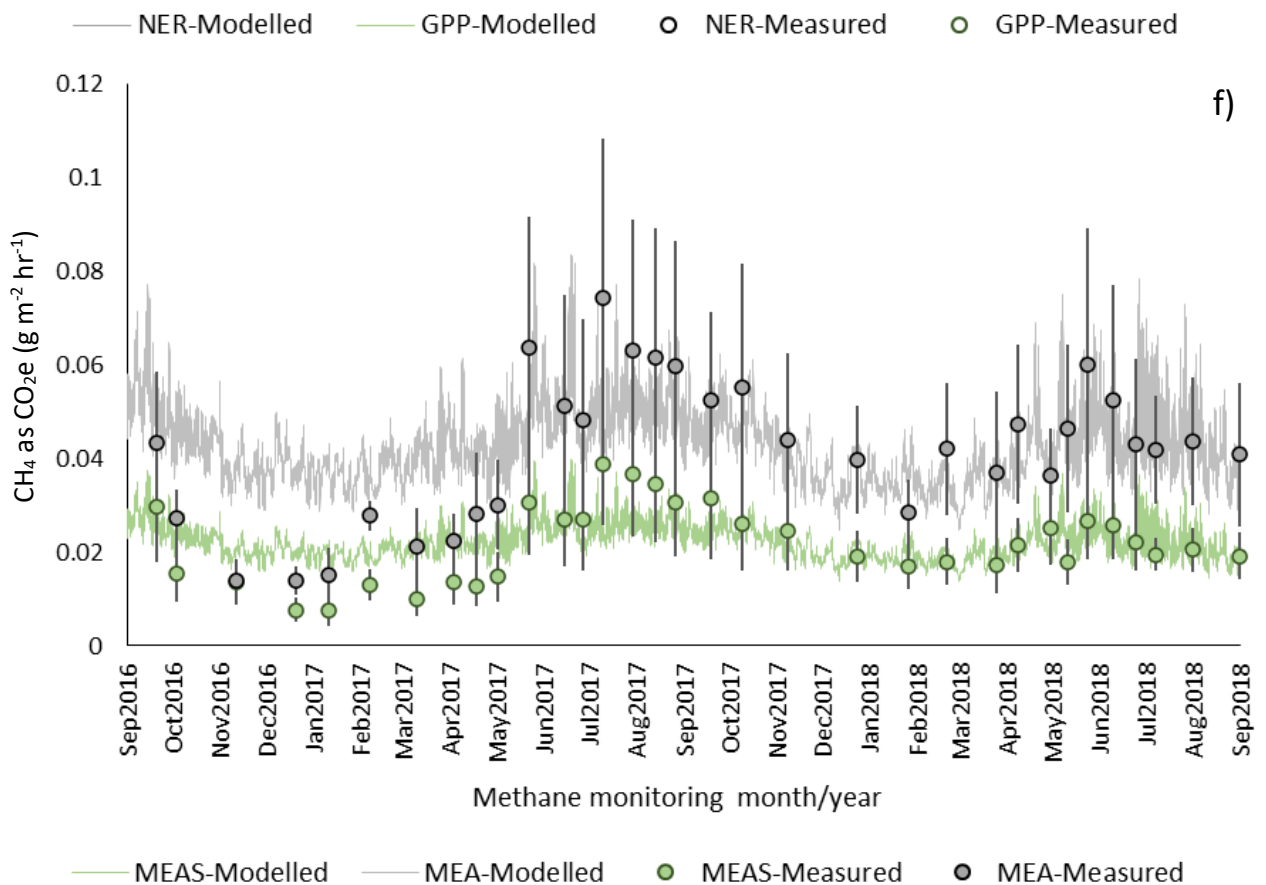
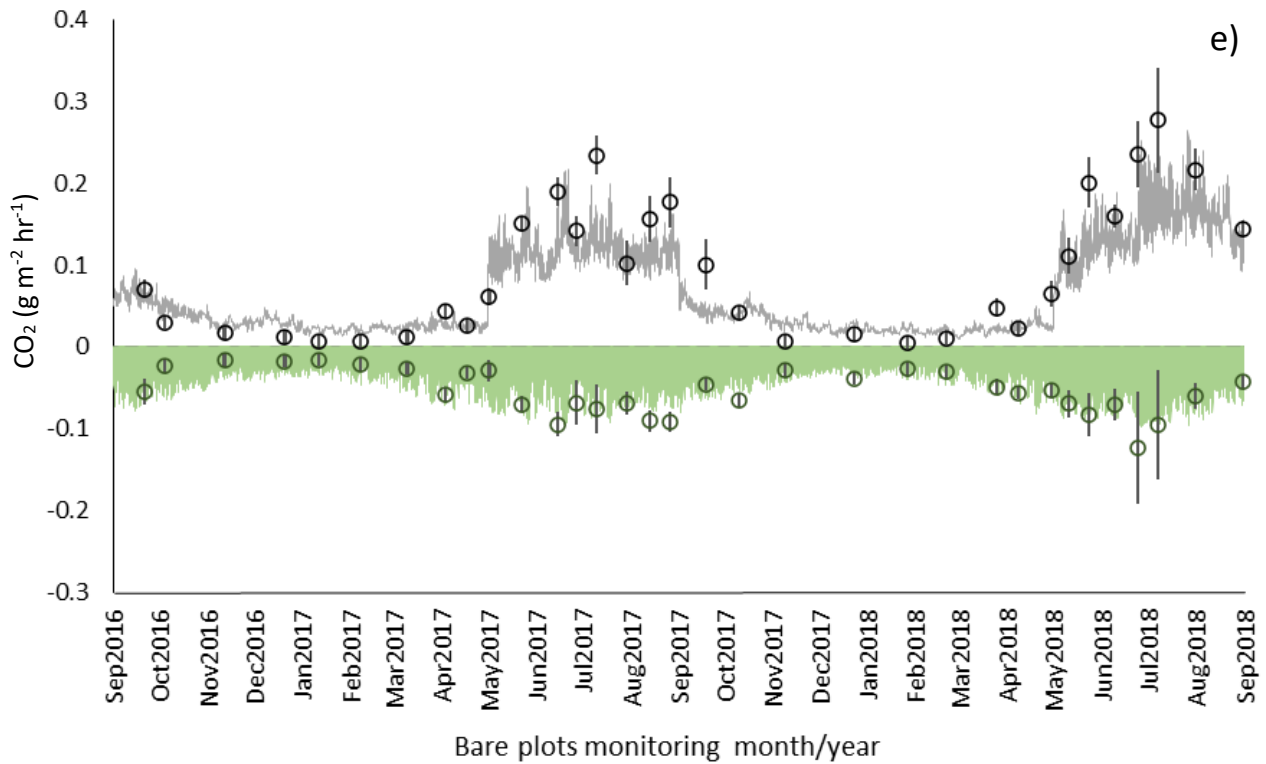


Figure 5 (continued). Modelled and measured Net Ecosystem Respiration (NER) (Rowson *et al.* 2013 model) and Gross Primary Productivity (GPP) (This Study model) on treatment e) BARE plots = bare peat control plots. Modelled and measured CH₄-CO₂e on f) mature plots. Lines show modelled hourly data, points show mean measurements ± SE.

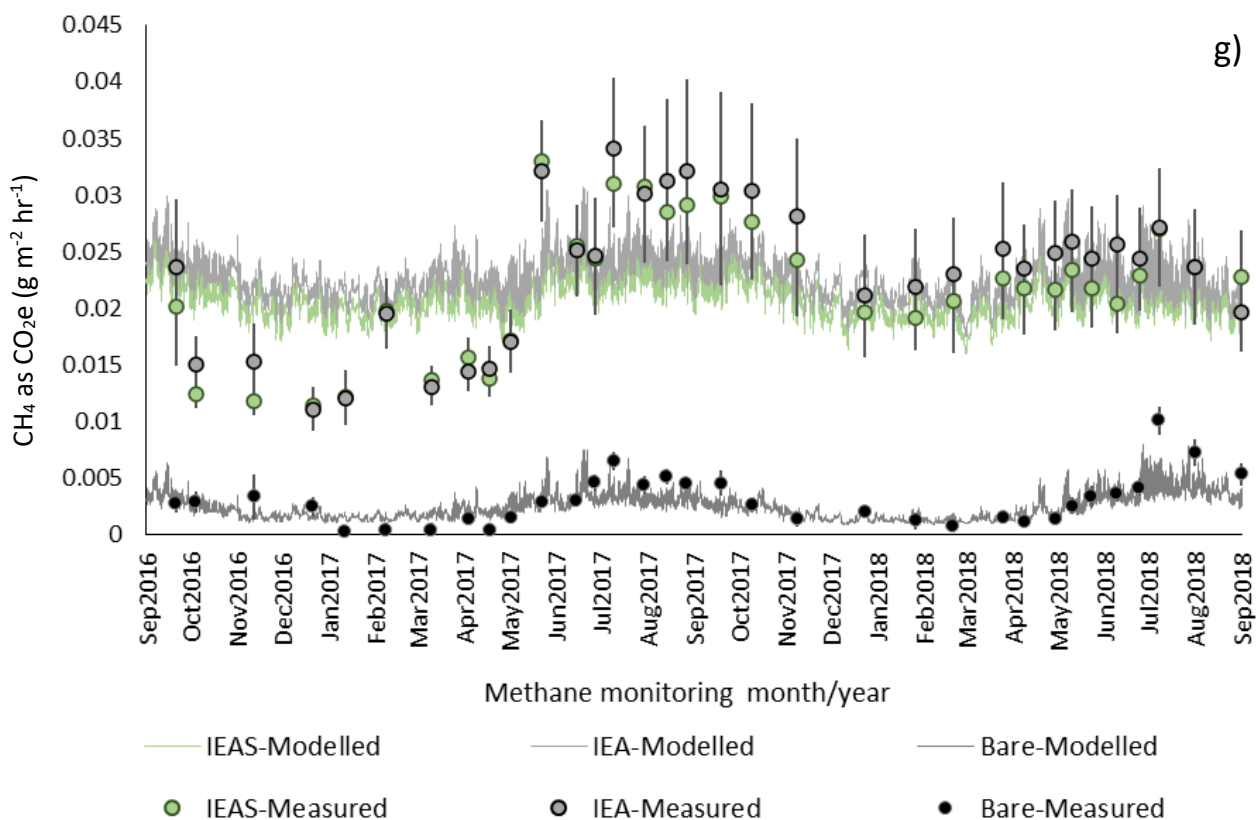


Figure 5 (continued). Modelled and measured CH₄-CO₂e on g) immature plots. Lines show modelled hourly data, points show mean measurements ± SE.

Modelled CGHG budgets

Between study years, annual NER in vegetated plots (Table 6) was similar for each treatment (IEAS $p < 0.05$; other treatments no significant difference (NS)). Both GPP (IEAS $p < 0.01$, IEA $p < 0.05$, other treatments $p < 0.001$) and consequently NEE ($p < 0.001$ throughout) were lower in Year 2, and methane flux converted to CO₂e also ($p < 0.001$ throughout). When CH₄-CO₂e flux was added to NEE to give an overall annual carbon greenhouse gas (CGHG) budget, there was a reduction in the Year 2 CGHG uptake in MEAS, MEA and IEAS plots ($p < 0.001$), and an increase in emission in IEA ($p < 0.001$) plots. In BARE plots, NER was higher in Year 2 ($p < 0.001$) and GPP was similar in both years (p NS) which increased NEE in Year 2 ($p < 0.001$); CH₄-CO₂e was also higher in Year 2 ($p < 0.001$) resulting in increased CGHG emission in Year 2 compared to Year 1 ($p < 0.001$). Methane emission from BARE plots was 11–12 % of that from MEAS, IEAS and IEA plots, and 6 % of that from MEA plots.

The difference in CGHG budgets between treatment groups (Table 6) was statistically significant in both Year 1 ($H(4) = 301.1$, $p < 0.001$) and Year 2 ($H(4) = 661.2$, $p < 0.001$). Post-hoc

Mann-Whitney pairwise tests showed statistically significant differences between all treatments ($p < 0.001$) apart from MEA and both IEA and BARE (p NS) in Year 1.

CGHG uptake was larger in plots of mature vegetation without *Sphagnum* (MEA > MEAS) in both years ($p < 0.001$) and larger in plots of immature vegetation with *Sphagnum* (IEAS > IEA) (both years $p < 0.001$). In all plots without *Sphagnum*, uptake was higher in mature than in immature vegetation throughout (MEA > IEA) (p NS in Year 1; $p < 0.001$ in Year 2). In all plots with *Sphagnum*, uptake was higher in mature vegetation in Year 1 (MEAS > IEAS) ($p < 0.001$) but higher in immature vegetation in year 2 (IEAS > MEAS) ($p < 0.001$).

The data showed an overall progression towards a CGHG sink function in this peatland restoration site during Year 1 (Figure A5), with high CGHG emission from bare peat and a net CGHG emission becoming a net uptake as vegetation colonised and matured. However, the drier conditions during Year 2 reduced CGHG uptake significantly, particularly in mature vegetation, and resulted in CGHG emission from plots of mature vegetation with *Sphagnum*.

Table 6. Treatment composition and characteristics with associated modelled annual sum flux measurements. MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*); MEA = mature vegetation (*E. angustifolium* only); IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*); IEA = immature vegetation (*E. angustifolium* only); WTD = water table depth (cm); NER = net ecosystem respiration; GPP = gross primary productivity; NEE = net ecosystem exchange; CO₂ equivalents of CH₄ were calculated by multiplying by Global Warming Potential (GWP)₁₀₀ of 28 and added to NEE values to give a CO₂e CGHG budget in g m⁻² yr⁻¹ (final column); values other than fluxes reported as means of measurements ± SD.

Treatment	Year	WTD (cm)	<i>Eriophorum angustifolium</i> (cm ³)	<i>Sphagnum</i> (cm ³)	NER (g m ⁻² yr ⁻¹)	GPP (g m ⁻² yr ⁻¹)	NEE (g m ⁻² yr ⁻¹)	Methane (g m ⁻² yr ⁻¹)	Methane as CO ₂ e (g m ⁻² yr ⁻¹)	CO ₂ e CGHG budget (g m ⁻² yr ⁻¹)
MEAS	1	5.88 ± 6.45	212.63 ± 126.29	5968.39 ± 2567.12	2067.44	-2622.53	-555.09	7.16	200.46	-354.63
	2	11.77 ± 17.21	214.27 ± 106.25	8223.62 ± 2851.15	2065.86	-2231.26	-165.40	6.62	185.45	20.05
	(mean)	9.30 ± 14.05	213.54 ± 115.02	7221.30 ± 2940.18	2066.65	-2426.89	-360.24	6.89	192.95	-167.29
MEA	1	5.88 ± 6.45	302.84 ± 132.25	0	3169.61	-4107.46	-937.85	13.66	382.53	-555.32
	2	11.77 ± 17.21	371.73 ± 114.66	0	3165.34	-3644.63	-479.30	12.78	357.77	-121.52
	(mean)	9.30 ± 14.05	341.11 ± 126.41	0	3167.47	-3876.05	-708.57	13.22	370.15	-338.42
IEAS	1	18.70 ± 14.47	68.39 ± 49.22	310.59 ± 157.31	1207.14	-1570.75	-363.61	6.66	186.52	-177.09
	2	18.69 ± 15.36	117.19 ± 70.20	975.72 ± 429.50	1237.25	-1495.38	-258.13	6.49	181.67	-76.47
	(mean)	18.69 ± 14.92	95.50 ± 66.14	822.23 ± 475.78	1222.19	-1533.07	-310.87	6.57	184.09	-126.78
IEA	1	18.70 ± 14.47	55.63 ± 42.58	0	1192.52	-1237.02	-44.50	7.11	199.08	154.59
	2	18.69 ± 15.36	82.37 ± 50.78	0	1216.15	-1192.39	23.76	7.03	196.86	220.62
	(mean)	18.69 ± 14.92	70.48 ± 48.95	0	1204.34	-1214.70	-10.37	7.07	197.97	187.61
BARE	1	18.70 ± 14.47	0	0	531.08	-198.69	332.39	0.75	21.02	353.42
	2	18.69 ± 15.36	0	0	587.54	-203.94	383.60	0.78	21.73	405.33
	(mean)	18.69 ± 14.92	0	0	559.31	-201.31	358.00	0.76	21.38	379.37

DISCUSSION

In Year 1 this study showed a progression from continual CGHG emission from bare peat, through a reduction in emissions on initial colonisation with bog vegetation (in this case *Eriophorum angustifolium*), to a large CGHG uptake by mature recolonising *E. angustifolium*, and a benefit from introduction of *Sphagnum* mosses to immature vegetation. However, in Year 2 with variable weather patterns and a long period of summer drought, the CGHG uptake was small, and areas of bare peat and sparse vegetation, particularly with no *Sphagnum* cover, showed increasing emissions of CGHG, and there was a change from CGHG uptake to emission in the mature *E. angustifolium* with *Sphagnum* treatment. This could suggest that the site has minimal resilience to anticipated climate change in the UK such as the increased frequency of hot summers (Lowe *et al.* 2018, Met Office 2019). However, although drought in the second year may have limited the potentially positive influence of increasing vegetation cover, the avoided CGHG losses through restoring the site (i.e., not leaving it bare) were large, so supporting hypothesis 1, that restoration of the site will result in a CGHG uptake compared to bare peat. This highlights the urgent nature of restoring degraded peatlands for best outcomes in terms of climate change mitigation targets (Nugent *et al.* 2019).

One of the aims of this study was to ascertain the influence of the type and maturity of vegetation on CGHG fluxes, but altered weather patterns between the two years of study influenced volume and condition of both *E. angustifolium* and *Sphagnum*, and thus their capacity for CGHG uptake. *E. angustifolium* growth and senescence followed expected seasonal trends in the first year of study, but growth stalled in the second summer in all plots but IEAS, indicating that the drought may have caused early senescence in the vascular plants (Bubier *et al.* 2003), and reduced their photosynthesis. The Year 2 summer drought also reduced *Sphagnum* volume in mature plots and caused severe surface desiccation, reducing photosynthetic potential (McNeil & Waddington 2003, Bortoluzzi *et al.* 2006, Rydin & Jeglum 2013, Helfter *et al.* 2014). Additionally, lower PAR in the spring of Year 2 (probably cloudier conditions) may have also limited photosynthesis (Lafleur *et al.* 2003, Loisel *et al.* 2012) and contributed to lower GPP for the whole year (Nijp *et al.* 2015).

Conversely, *Sphagnum* in immature plots grew in volume throughout the study period, with mesh shading to support early establishment and some

environmental protection provided through being lower in the *E. angustifolium* sward than *Sphagnum* within mature *E. angustifolium*. This may have helped retain soil moisture and reduce evapotranspiration for a healthy layer of *Sphagnum*, but also appeared to favour continued *E. angustifolium* growth and development in these plots during the drought period. Mesh shading was used to replicate straw mulching but is not likely to be employed in large-scale restoration works, where straw-mulching is routinely used.

In mature vegetation, the volume of *E. angustifolium* was less in plots with *Sphagnum* than without, which may be related to reduction in exposure of *E. angustifolium* leaves to sunlight as the *Sphagnum* grew and increasingly covered them, or a greater capacity of *Sphagnum* to harvest nutrients for growth (Malmer *et al.* 2003, Bragazza *et al.* 2004, Fritz *et al.* 2014). Immature *Sphagnum* had not reached a height at which it competed with *E. angustifolium* for light. The water table was higher in plots with mature vegetation than those with immature vegetation and bare peat. Wilson *et al.* (2013) also found this, and potential explanations are that evaporation is reduced through increased shade from dense *E. angustifolium* (Price *et al.* 2003), or that a higher water table supports proliferation of *E. angustifolium* (Rochefort *et al.* 2016). Topographical differences between collar locations were not measured, but may have influenced plant growth.

CO₂ uptake through GPP was greater in plots of mature *E. angustifolium* only, which had the greatest volume of *E. angustifolium* overall, suggesting that Hypothesis 2, CGHG uptake will be greater with maturity of vegetation, was supported. But the overall picture was more complex. NER emission was also highest in these plots, and greater than in plots with immature vegetation or bare peat, and rates of NER and GPP were closely related. This accords with studies suggesting NER is higher in vegetated than in BARE plots and is related to litterfall, temperature and rainfall (Bortoluzzi *et al.* 2006, Evans *et al.* 2016, Jordan *et al.* 2016), but the most important factor may be inputs of carbon from photosynthesis (Bond-Lamberty *et al.* 2004). However, greater NER emission was also related to warmer, drier conditions, which concurs with most literature sources (e.g., Danevčič *et al.* 2010, Wang *et al.* 2014), particularly for bare peat (Bortoluzzi *et al.* 2006) although this can alter depending on the plant assemblage in a heterogeneous peatland system (Juszczak *et al.* 2013). The NER increase in BARE plots each year could be related to the encroachment of surrounding vegetation, and root growth within the

column of bare peat inside the collar, even though surface vascular plant growth was removed, but is more likely due to greater microbial decomposition in drier, warmer conditions (Juszczak *et al.* 2013). Algae and acrocarpous bryophytes (no *Sphagnum* growth) were not removed, however, as this is a natural progression of bare peat cover, and this may have influenced carbon cycling in these plots.

Methane emissions (as CO₂e) considerably reduced CGHG uptake in each vegetated treatment, highlighting the importance of including methane in GHG studies (Bussell *et al.* 2010, Haddaway *et al.* 2014). However, methane fluxes were generally mid-range to low in all treatments compared to some studies on rewetted sites using instantaneous measurements (e.g., Beyer & Höper 2015, Davidson *et al.* 2016, Evans *et al.* 2016), which is perhaps to be expected in a site where microbial communities are still recovering from the effects of long-term drainage during peat cutting and subsequent evapotranspiration from scrub cover (Andersen *et al.* 2013, Juottonen *et al.* 2015, Nugent *et al.* 2018) and perhaps a reduction in substrate nutrient availability (Basiliko *et al.* 2007) prior to restoration ten years ago. It might be expected that methane fluxes in this study would increase as the site matures (in the short term) with more plant growth, plant litter and a higher, more stable water table, leading to greater availability of labile carbon (Glatzel *et al.* 2004, Lafleur *et al.* 2005, Urbanová *et al.* 2011): measured seasonal results in this study prior to the Year 2 summer drought supported that trend. MEA plots had greater volumes of *E. angustifolium* and approximately twice the methane emission of other vegetated plots, supporting Hypothesis 3, that greater volumes of *E. angustifolium* will result in greater emission of methane. However, overall methane fluxes in the second year with drought were lower throughout vegetated plots compared to the previous wet year, in accordance with the accepted view that methane flux declines (CH₄ oxidises) in dry sites (Danevčič *et al.* 2010, Turetsky *et al.* 2014, Abdalla *et al.* 2016). There was no particular relationship between high water table and high methane emissions in vegetated plots overall, concurring with other studies, e.g., Wilson *et al.* (2022), who found the main driver of CH₄ flux on a rewetted site to be soil temperature, but contrary to earlier empirical evidence (Glatzel *et al.* 2004, Danevčič *et al.* 2010, Urbanová *et al.* 2011, Evans *et al.* 2016).

Methane flux was higher in vegetated plots without *Sphagnum*, even in immature vegetation where *E. angustifolium* volume was higher in plots with *Sphagnum* than without, supporting Hypothesis 4, that the presence of *Sphagnum* moss will reduce

the magnitude of methane emission. Flux from bare plots was 9 % that of vegetated plots overall. These results concur with Bortoluzzi *et al.* (2006) who reported the rank of highest to lowest fluxes to be *Eriophorum*-dominated, *Sphagnum*-dominated, then bare plots, and Couwenberg *et al.* (2011) who found a strong relationship between methane flux and the density of aerenchymatous leaves. Methane flux appears to be related to the amount of *E. angustifolium*, but is also reduced when *Sphagnum* is present, suggesting some methanotrophic consumption of methane in the *Sphagnum* layer (Kip *et al.* 2010, Larmola *et al.* 2010, van Winden *et al.* 2012, Nugent *et al.* 2018).

In common with Leppälä *et al.* (2011), this study found that reduction in CGHG uptake in a dry year compared to the previous wet year was driven more by changes in GPP than NER. However, plant dynamics were a complex factor. Greater volumes of *E. angustifolium* appeared to be related to greater CGHG uptake. This is partly contrary to findings of Kivimäki *et al.* (2008) that stands of mixed sedges and *Sphagnum* sequestered more carbon than those of sedges alone due to lower NER, but the maturity of the vegetation is a factor in our study. Wilson *et al.* (2013) found greater NEE in plots with sedges when compared to those with *Sphagnum* only. Moreover, Tuittila *et al.* (1999) suggested that a restored site colonised with mature *Eriophorum* (*E. vaginatum*) was a carbon sink resilient to interannual changes in weather. However, other studies found that NEE was greater in rewetted *Sphagnum*-dominated than in sedge-dominated sites (Beyer & Höper 2015, Evans *et al.* 2016, Renou-Wilson *et al.* 2019) due to a lower NER to GPP ratio, and the presence of *Sphagnum* may reduce NER by retaining moisture (Waddington & Warner 2001). In our study, there was a lower NER to GPP ratio each year in *E. angustifolium*-only than with *Sphagnum* in mature stands, but the reverse was so in immature stands, with the lowest NER to GPP ratio overall each year in immature *E. angustifolium* with *Sphagnum*. An open sward of immature *E. angustifolium* emitted CGHG, increasingly so in the drought year, but with a layer of *Sphagnum* it became a CGHG sink each year.

Lower CGHG emission through NER and higher uptake through GPP in immature plots with *Sphagnum* than without suggests an effect of both increased moisture retention (Waddington & Warner 2001) and more plant material on the peat substrate. This may indicate that establishment of a layer of *Sphagnum* is more crucial in immature than in mature vegetation, in terms of CGHG uptake, and so efforts to create a beneficial microclimate at the peat surface (e.g., mulch, nurse planting, etc.) should be one of the

fundamental processes for initial stages of peatland restoration (Quinty & Rochefort 2003, Groeneveld *et al.* 2007, Waddington *et al.* 2010, Pouliot *et al.* 2011). Early micropropagated mixed-species *Sphagnum* introduction into *E. angustifolium* also appears to create a mutually supportive environment for both plants, whereas attempting to introduce it when *E. angustifolium* is already well-established does not seem to promote good *Sphagnum* outcomes, particularly in dry conditions.

The large range in collar flux measurement within treatments (noted by Bortoluzzi *et al.* (2006) in their study, and seen in data from other sources, e.g., Wilson *et al.* 2013, Beyer & Höper 2015, Renou-Wilson *et al.* 2019), demonstrates the heterogeneity of the site, the complex nature of associations between carbon cycling in degraded peatlands under restoration measures and fluctuations in environmental factors, and perhaps that using vegetation type and density as a proxy for carbon balance measurements may not capture the CGHG state of individual sites sufficiently.

This study found the *E. angustifolium*-dominated area of Cadishead Moss with and without *Sphagnum* introduction to be an overall net CGHG sink, despite the methane emissions, in Year 1 and an overall net CGHG source in Year 2, which included a summer drought. The mean (SE) CO₂e CGHG emission of vegetated monitoring points was -233.11 (150.56) g m⁻² yr⁻¹ in Year 1 and 10.67 (75.96) g m⁻² yr⁻¹ in Year 2. This supported Hypothesis 5, that periods of drought, which generate a low water table, will have a deleterious effect on site CO₂ uptake. The mean (SE) yearly CO₂e CGHG emission from bare peat of 379.37 (25.96) g m⁻² yr⁻¹ shows the benefits of restoration in terms of avoided CGHG losses (Worrall *et al.* 2011, Renou-Wilson *et al.* 2019). The CO₂e sink strength in vegetated plots in Year 1 is in the mid-range of some other similar restored bogs (e.g., those studied by Drewer *et al.* 2010, Beyer & Höper 2015 and Renou-Wilson *et al.* 2019). The findings from this study are contrary to those of Evans *et al.* (2016) at the nearby Astley Moss (rewetted cut-over bog), where measurements were taken on a generally inundated part of the site, and very high methane emissions (43.7 g m⁻² yr⁻¹) pushed the CO₂e NEE sink of -336 g m⁻² yr⁻¹ (revised to -41 g m⁻² yr⁻¹ across the entire site based on vegetation assemblage) into a site CGHG source. More data are needed on lowland bogs under restoration to further refine the inventory of greenhouse gas emission factors for UK peatlands (Evans *et al.* 2017), and our study can contribute to that.

This study site is not yet in equilibrium, has a widely fluctuating WTD, and changed over the study

period in terms of vegetation cover and density. Few studies, assessing GHG fluxes in relation to type of vegetation (Strack & Zubak 2013, Wilson *et al.* 2013, Renou-Wilson *et al.* 2019), and over time (Waddington *et al.* 2010), fully address the question of the dynamic nature of vegetation on fluxes in a single peatland system under restoration measures over time, although there are some good, recent examples (e.g., Nugent *et al.* 2018, Nugent *et al.* 2019). This broader, integrated approach is worth exploring in more depth, particularly when funding for restoration work may depend on evidence for change over short timescales.

The study area had high peat NO₃ and NH₄ levels (Table 1), which could be related to intermittent aerobic conditions (Urbanova *et al.* 2011), but Cadishead Moss is close to the large conurbation of Greater Manchester, so may have legacy pollution effects from the Industrial Revolution (Garcés-Pastor *et al.* 2023) as well as current effects from regional oxidised and reduced nitrogen pollution. Modelled nitrogen deposition to the site is approximately 18.9 kg ha⁻¹ yr⁻¹, well above empirical critical loads for nitrogen for lowland raised bogs of 5–10 kg ha⁻¹ yr⁻¹ (UKCEH 2023). Low water table is of particular concern, as the influence of nitrogen deposition is increased when concentrated in solution (Pearce & Van der Wal 2008) and there may be cumulative N-load effects (Sheppard *et al.* 2014), which compromise bryophyte growth, increase algal growth (Payne *et al.* 2013), and make scrub development more likely on a dry peatland site with high atmospheric nitrogen deposition (Krupa 2003, Bubier *et al.* 2007).

Significant proportions of the top 50 cm of peat cores taken were black, oxidised, rough-textured peat, showing evidence of the compaction and hydrological instability typical of damaged peatlands where the acrotelm has been removed (Price *et al.* 2003, Lindsay & Clough 2016). Moreover, all bare plots, and some plots with immature vegetation, cracked during the summer drought, which is a likely sign of humification, and no doubt allowed greater evaporation down the peat profile (Lindsay & Clough 2016). Because this area of the site has been previously mechanically scraped with none of even the original block-cut surface remaining, rehabilitation to ecohydrological function, particularly in the short term, is questionable (Price *et al.* 2003). Long-term degradation of the site has resulted in poor-quality surface and sub-surface peats, which are likely to contribute to poor hydrological control and continue to create obstacles to restoration and reduced capacity for CGHG uptake. Chemical analysis of the changing

environment on this degraded site over time, particularly with integrated studies of surface peats, plants and water, could be used to quantify restoration progress (Andersen *et al.* 2010), and would allow greater understanding of the nutrient cycling and microbial activity underpinning its capacity for CGHG sequestration. However, particular focus should be concentrated on improving hydrological control to maintain higher WTD during dry periods to promote long-term recovery.

If climate change continues to affect weather patterns, summer drought may become more common (Lowe *et al.* 2018, Met Office 2019). If so, it is likely that the CGHG sink function of peatlands under restoration will reduce unless greater resilience, particularly in terms of maintaining water table levels to support *Sphagnum* proliferation, can be engineered so that a functional acrotelm redevelops in the long term.

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AUTHOR CONTRIBUTIONS

ATK co-originated and planned the work, undertook all field and laboratory work, wrote the drafts and final paper, and is the lead author; CDF, JGR and SJMC had academic oversight, co-originated the work, assisted in planning and installing field equipment, and commented on all drafts; NAW co-originated the work, supplied and applied *Sphagnum* materials, assisted in planning, and commented on drafts.

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Appendix

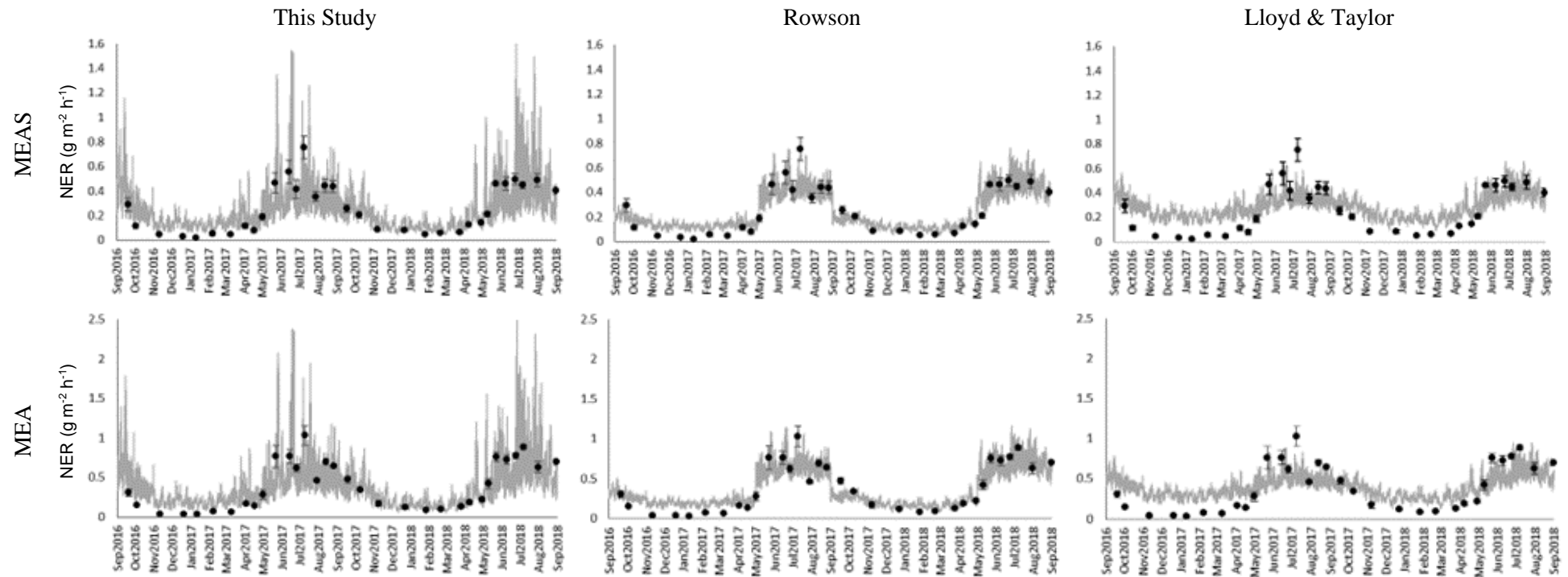


Figure A1. Graphs showing goodness of fit between mean measured and variously modelled data for NER by treatment groups. Values measured (at intervals of two weeks to one month) are shown by points with error bars (SE), superposed on a graph of hourly values modelled using the methods of This Study, Rowson *et al.* (2013) or Lloyd & Taylor (1994) + WTD. The treatments are: MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*) and MEA = mature vegetation (*E. angustifolium* only).

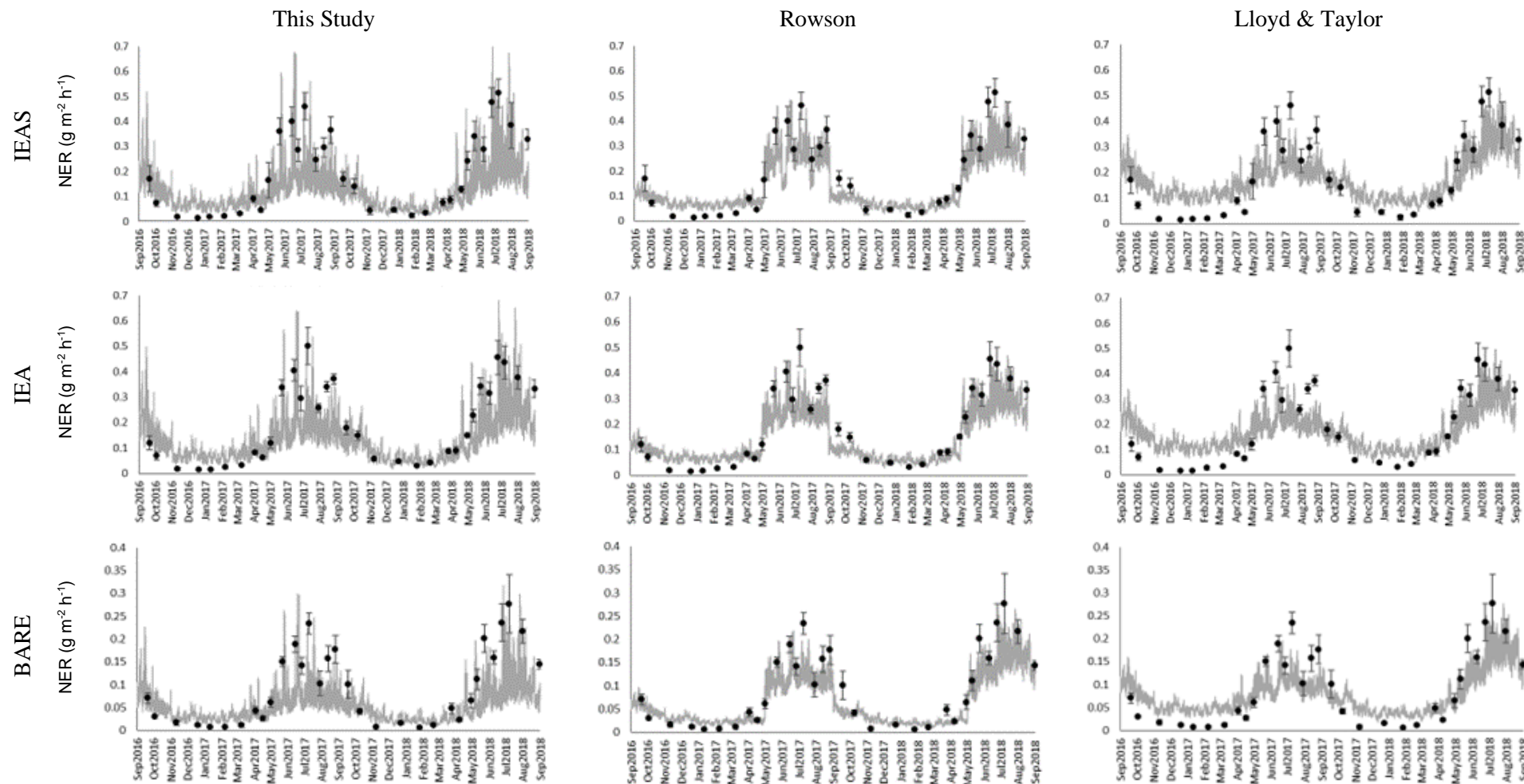


Figure A2. Graphs showing goodness of fit between mean measured and variously modelled data for NER by treatment groups. Values measured (at intervals of two weeks to one month) are shown by points with error bars (SE), superposed on a graph of hourly values modelled using the methods of This Study, Rowson *et al.* (2013) or Lloyd & Taylor (1994) + WTD. The treatments are: IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*), IEA = immature vegetation (*E. angustifolium* only) and BARE = bare peat control plots.



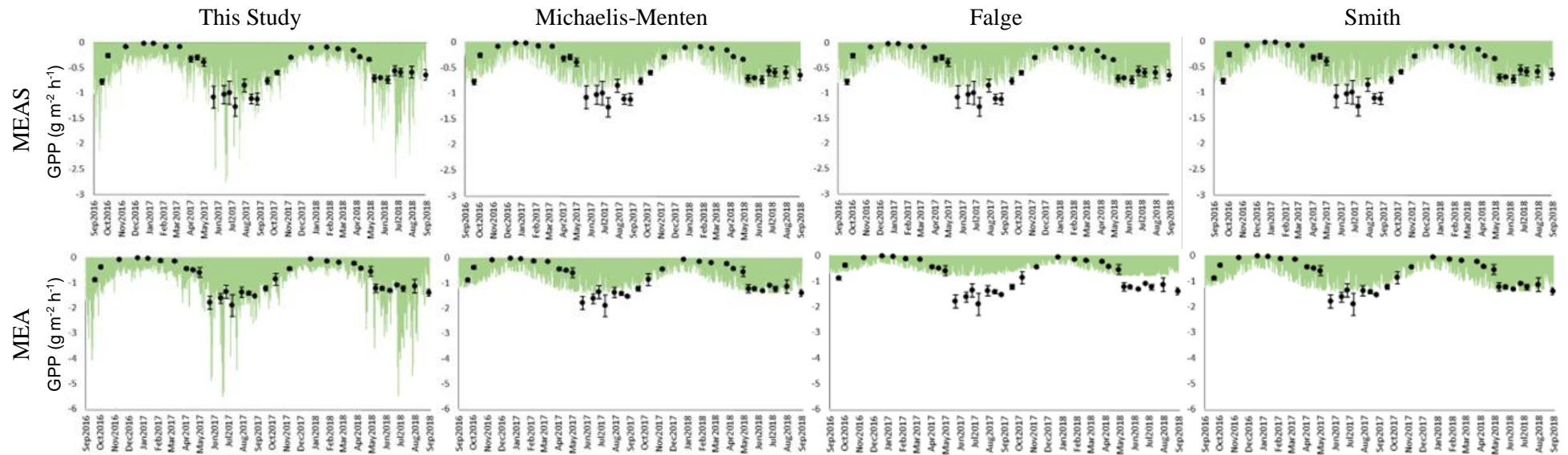


Figure A3. Graphs showing goodness of fit between mean measured and variously modelled data for GPP by treatment groups. Values measured (at intervals of two weeks to one month) are shown by points with error bars (SE), superposed on a graph of hourly values modelled using the methods of This Study, Michaelis & Menten (1913), Falge *et al.* (2001) or Smith (1936). The treatments are: MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*) and MEA = mature vegetation (*E. angustifolium* only).



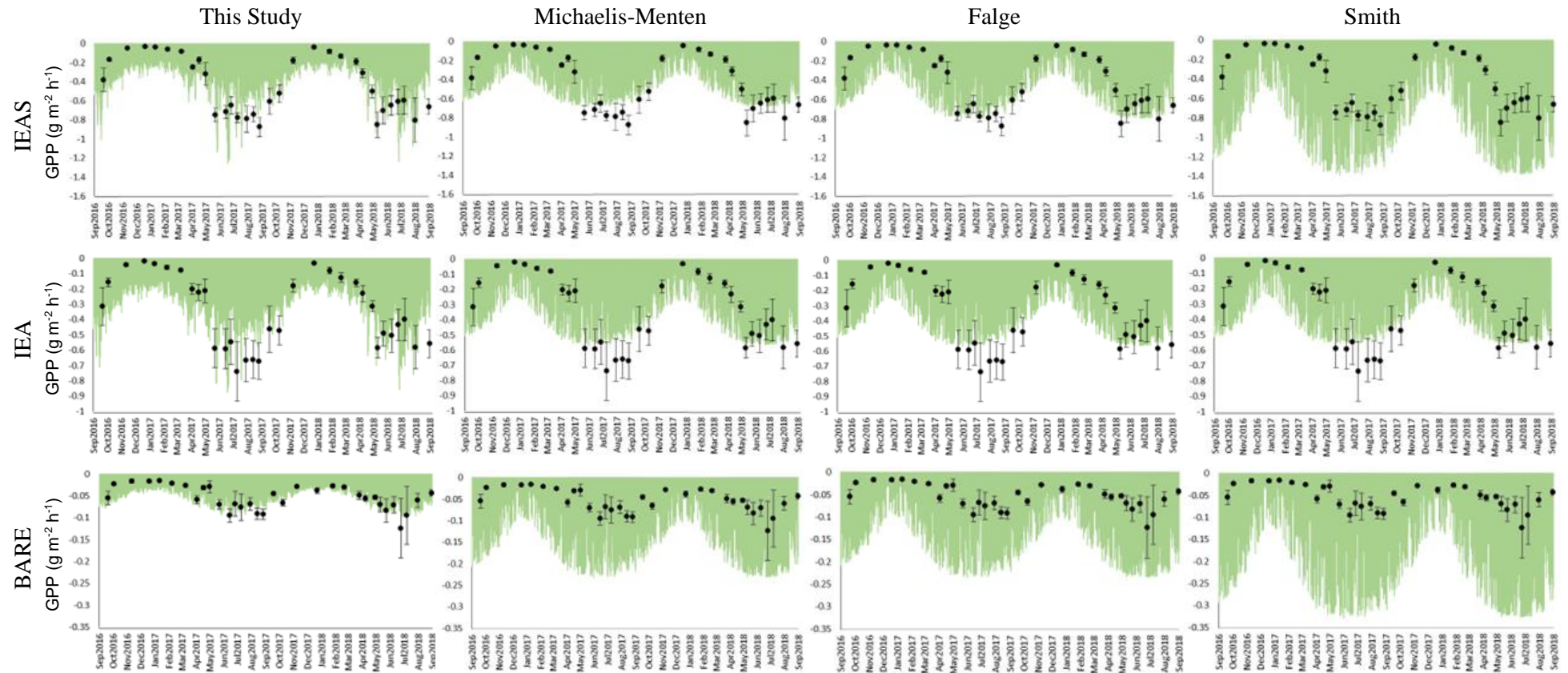


Figure A4. Graphs showing goodness of fit between mean measured and variously modelled data for GPP by treatment groups. Values measured (at intervals of two weeks to one month) are shown by points with error bars (SE), superposed on a graph of hourly values modelled using the methods of This Study, Michaelis & Menten (1913), Falge *et al.* (2001) or Smith (1936). The treatments are: IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*), IEA = immature vegetation (*E. angustifolium* only) and BARE = bare peat control plots.



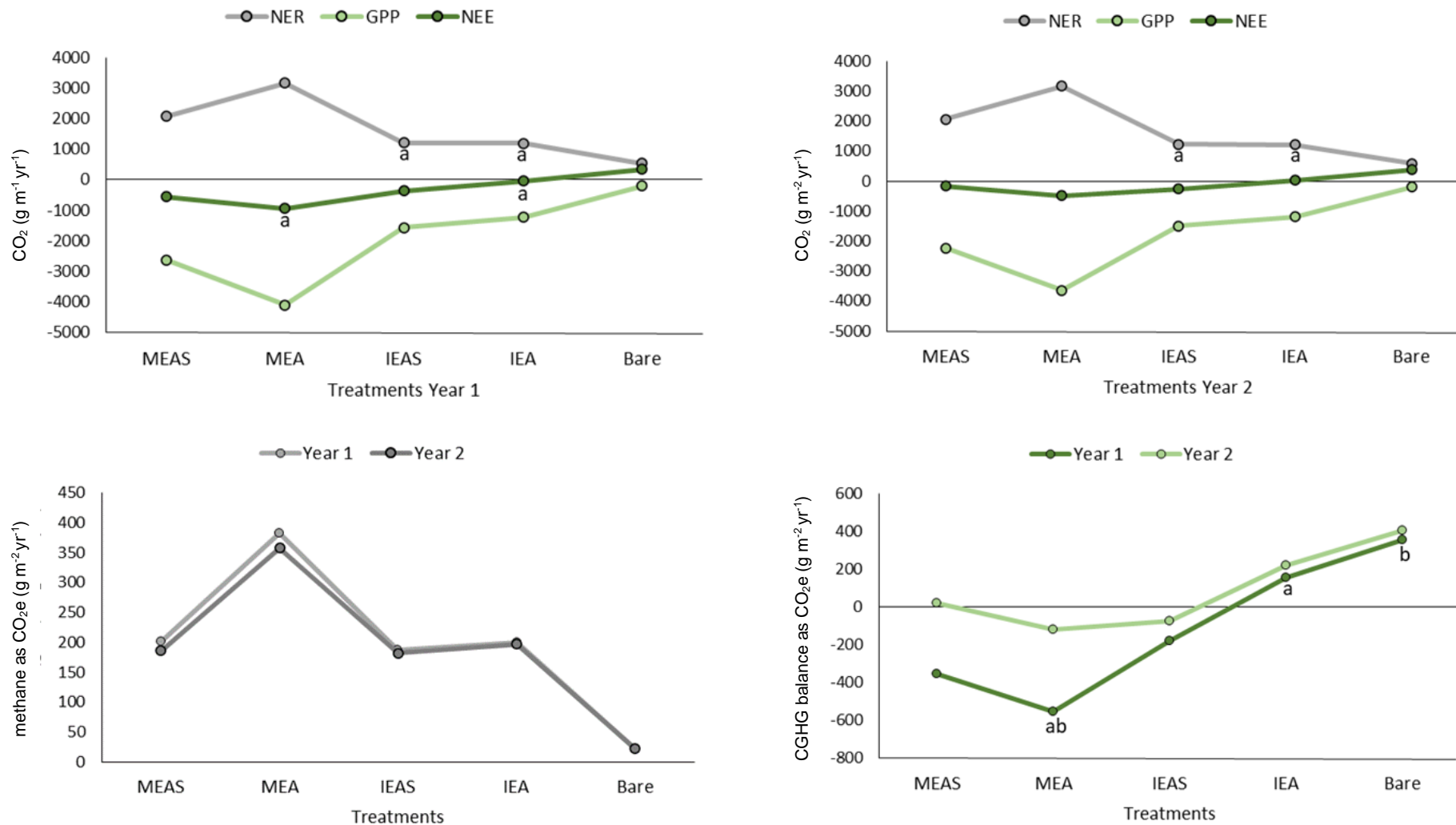


Figure A5. Modelled yearly fluxes comparing treatments. Top row: NER, GPP and NEE in Year 1 and Year 2; bottom left: methane as CO₂e in Years 1 and 2; and bottom right: CGHG balance as CO₂e in Years 1 and 2. The treatments are: MEAS = mature vegetation (*E. angustifolium* with *Sphagnum*); MEA = mature vegetation (*E. angustifolium* only); IEAS = immature vegetation (*E. angustifolium* with *Sphagnum*); IEA = immature vegetation (*E. angustifolium* only); Bare = bare peat. Shared letters below each flux line indicate no significant statistical difference between treatments.

