

ANSWER TO REVIEWER #1

We thank reviewer #1 for taking the time to read our manuscript and for raising two interesting questions, which we endeavour to answer here:

1. The scientific significance of the paper is limited to the British Isles and therefore does not significantly broaden our knowledge in the field. Would this model/concept be applicable to other type of peatland initiation? For example to raised bogs to areas of large peatland extends (Canada, Siberia etc.)?

Interestingly, the debate over the initiation causes of blanket bogs is limited to the British Isles. Blanket bogs initiated also in other parts of the world where anthropogenic influences were non-existent or very sparse, but past papers seems to suggest British blanket bogs are “different” from those. Moreover, this incorrect view continues to be influential in the UK and, in our experience of discussions involving local stakeholders, to cloud understanding of the overall control of blanket bog distribution and thus also understanding of the importance of considering climate change when planning conservation measures.

Thus we attempt, as the reviewer says, to end a rather long-standing debate. This is the reason for focusing solely on the British Isles.

We have used PeatStash to model the distribution of other types of peatlands using different bioclimatic thresholds. Variants of the model with different threshold definitions perform remarkably well in predicting the broad geographic distributions of other types of peatlands, including the raised bogs of the northern latitudes, and even tropical peatlands. However, there is an important limitation on these results because of topographical controls on peatland extent: without adding a topographic component, the model greatly overestimates local peatland extent.

Therefore, we choose to focus on blanket bogs. These peatlands uniquely are not limited to flat areas or the bottom of valleys, as they are able to extend to sloping ground, and when present, typically “blanket” the whole landscape.

2. Also, is the PeatStash model really needed to draw one of the two main conclusion points (L1-10, p4821)? Because these conclusion could simply be drawn from the pollen hydroclimatic reconstruction, right?

If the climatic thresholds were solely determined by MAT, MTWA and MAP, one could draw the same conclusions from the pollen reconstructions directly. However, we use the Peatstash model because the model represents the moisture regime by a moisture index (MI), which requires a more complex calculation (for potential evapotranspiration) that is more appropriate in a process sense and also provides a threshold that fits the present distributions more

accurately than MAP. Changes in MI, in turn, can be estimated from changes in the alternative moisture index α , for which pollen-based reconstructions exist. The use of an explicit model further allowed us to make quantitative predictions based on climate model simulations for the mid-Holocene and to show conclusions consistent with the pollen-based approach.

ANSWER TO REVIEWER #2

We thank reviewer #2 for raising several interesting issues and questions, which we respond to here:

1. My main concern about this study is the restricted area targeted by this modeling exercise. The authors could broaden the impact of their study by emphasizing the potential role of the British blanket bogs as analogs for bogs worldwide.

The reason we focus solely on the British Isles is because the debate over the whether the initiation of blanket bogs is human induced or caused by climate change is basically limited to this area. Even when studies from other regions have raised (and usually dismissed) the possibility that humans caused blanket bog formation, they have cited papers about the UK as proof that this could be the case. The view that humans produced these landscapes continues to be influential in the UK and, in our experience of discussions involving local stakeholders, to cloud understanding of the overall control of blanket bog distribution and thus also understanding of the importance of considering climate change when planning conservation measures. However, we agree with the reviewer that the “unique” nature of the UK debate could have been better emphasised and we have therefore added two sentences in the introduction (beginning of the second paragraph) to make this clearer, as follows:

The global distribution of blanket bogs today is confined to cool, wet climates (Gallego-Sala and Prentice, 2013). The initiation of blanket bog formation during the Holocene is regionally asynchronous, and in most regions has been found to coincide with a shift towards cooler, wetter climates (Zaretskya et al., 2001, Dirksen et al, 2012). However, there has been considerable debate about the cause of Holocene blanket-bog initiation in the UK.

We have also added a sentence in the final section to emphasise this:

Climatic control of blanket-bog formation in the UK is consistent with evidence from other parts of the world that blanket-bog initiation occurred in response to climate change and that their current distribution is strongly controlled by climatic conditions.

2. Furthermore their role in a context of changing climate could be strengthened as well. This could be done in the introduction and conclusion.

Our concern in this paper was to address a palaeoecological question that has not been satisfactorily answered in the literature, despite being a major focus for research for over 40 years. The role of blanket bogs in the context of a changing climate has been addressed in Gallego-Sala and Prentice, 2013. However, we agree that the survival of blanket bogs as an ecosystem will be affected by future climate changes and perhaps, by showing that by their past evolution can be satisfactorily explained by climate changes and does not require human intervention, our paper contributes to emphasising the climate sensitivity of these ecosystems. In view of this, we have added a final sentence to the manuscript to indicate why our findings might be relevant to the future climate impact debate around blanket bogs, following on from the existing text as follows:

Climatic control of blanket-bog formation in the UK is consistent with evidence from other parts of the world that blanket-bog initiation occurred in response to climate change and that their current distribution is strongly controlled by climatic conditions. It raises an important issue about the fate of this unique ecosystem under future climate change. Our work supports previous analyses that suggest they will require careful management given that their continued growth may be threatened by large-scale shifts in climate in some regions of the UK (Clark et al., 2010; House et al., 2010; Gallego-Sala et al., 2010) and worldwide (Gallego-Sala and Prentice, 2013).

3. If feasible, another option for broadening the impact of this study could be to use the PeatStash model to evaluate what would be the projected repartition of bogs in Britain and then worldwide for the next 100 years depending of the different climatic scenarios.

The issue of what will happen to blanket bogs in the future has already been addressed in Gallego-Sala and Prentice, 2013. We have made this clearer in the text added in response to comment 2. Here we focus on the initiation of blanket bogs.

4. How the uncertainties associated with the MAT, MTWA, MAP pollen reconstructions are taken into account in the modeling experiments? How do they transfer into uncertainties in the blanket bog repartition?

We use the pollen-based reconstructions as a “reality check” on the results obtained using the climate model simulations, in the sense that we have made sure that the simulated changes are consistent with the pollen-based reconstructions for those grid-cells where there are pollen-based reconstructions and in the sense that the simulation driven by the pollen-based reconstructions

produces a similar result. We took this approach because, despite the apparent wealth of pollen data from the UK, the number of grid cells for which we have quantitative climate reconstructions is still limited and thus there is some interpolation involved in producing inputs for PeatSTASH. In contrast, the climate models provide “global” inputs. We rely on the ensemble of climate simulations to provide us with a measure of the probability of climate being suitable in any one location for blanket bog to occur. As we said in the paper, there are uncertainties quoted for the gridded pollen-based reconstructions: the average values of these are 0.04 for α , 112 mm for mean annual rainfall and 1 °C for MTWA/MTCO. We did not run separate simulations using the range of uncertainties because these uncertainties are less than the inter-model differences between the simulations, and therefore our probability distribution already encompasses a larger range of uncertainty. We agree that it would be useful to clarify this point, as so we have expanded the text at the beginning of the methods section to clarify our approach as follows:

Pollen-based reconstructions provide an independent source of **information. However, their distribution is not continuous across the whole of the UK and the necessity to interpolate between reconstructions at individual sites could introduce uncertainty (Bartlein et al., 2011). Nevertheless, this information provides a useful check of the reliability of the simulated climates at the location of the sites and an alternative scenario of climate change. We therefore used both the climate-model ensemble and the pollen-based reconstructions** to obtain mid-Holocene climate estimates to drive PeatSTASH.

We have also added a sentence in section 2.3 as follows:

..... climatology (<http://www.cru.uea.ac.uk>). **We do not account for reconstruction uncertainties in this application because they are smaller than the differences between the climate-model scenarios.**

In our discussion, we already comment on the fact that the simulated climates are consistent with the pollen-based reconstructions (page 4819, line 15 et seq.).

5. Then, could the authors emphasize the novelty of this manuscript with that of the previous studies by the same authors: Gallego-Sala et al., 2010; Gallego-Sala and Prentice, 2013?

The study by Gallego-Sala et al., 2010 shows that it is possible to explain the distribution of blanket bogs in the UK using climate information and documents the model that is used here to simulate Holocene bog initiation. It also shows the likely impact of future climate changes on blanket bogs in the UK. The study by Gallego-Sala and Prentice, 2013 expands this analysis and modelling exercise to

the world. Although these two papers use the same modelling tool as the current paper (PeatSTASH), this paper applies this tool to answer an entirely different question namely: was human invention required to cause blanket-bog initiation in the UK during the Holocene? This kind of application of the model is very worthwhile because it answers a longstanding debate which could be addressed in no other way.

LIST OF CHANGES

We have made the following changes to the manuscript:

1. We have added two sentences in the introduction (beginning of the second paragraph), as follows:

The global distribution of blanket bogs today is confined to cool, wet climates (Gallego-Sala and Prentice, 2013). The initiation of blanket bog formation during the Holocene is regionally asynchronous, and in most regional has been found to coincide with a shift towards cooler, wetter climates (Zaretskia et al., 2001, Dirksen et al, 2012). However, there has been considerable debate about the cause of Holocene blanket-bog initiation in the UK.

2. We have also added a sentence in the final section to emphasise this:

Climatic control of blanket-bog formation in the UK is consistent with evidence from other parts of the world that blanket-bog initiation occurred in response to climate change and that their current distribution is strongly controlled by climatic conditions.

3. We have added a final sentence to the manuscript to indicate why our findings might be relevant to the future climate impact debate around blanket bogs, following on from the existing text as follows:

Climatic control of blanket-bog formation in the UK is consistent with evidence from other parts of the world that blanket-bog initiation occurred in response to climate change and that their current distribution is strongly controlled by climatic conditions. It raises an important issue about the fate of this unique ecosystem under future climate change. Our work supports previous analyses that suggest they will require careful management given that their continued growth may be threatened by large-scale shifts in climate in some regions of the UK (Clark et al., 2010; House et al., 2010; Gallego-Sala et al., 2010) and worldwide (Gallego-Sala and Prentice, 2013).

4. We have expanded the text at the beginning of the methods section to clarify our approach as follows:

Pollen-based reconstructions provide an independent source of **information**. **However, their distribution is not continuous across the whole of the UK and the necessity to interpolate between reconstructions at individual sites could introduce uncertainty (Bartlein et al., 2011). Nevertheless, this information provides a useful check of the reliability of the simulated climates at the location of the sites and an alternative scenario of climate change. We therefore used both the climate-model ensemble and the pollen-based reconstructions to obtain mid-Holocene climate estimates to drive PeatSTASH.**

5. We have also added a sentence in section 2.3 as follows:

..... climatology (<http://www.cru.uea.ac.uk>). **We do not account for reconstruction uncertainties in this application because they are smaller than the differences between the climate-model scenarios.**

6. We have added the appropriate additional references.

All these changes are highlighted in the following manuscript version.

Climate-driven expansion of blanket bogs in Britain during the Holocene

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Abstract

Blanket bog occupies approximately 6% of the area of the UK today. The Holocene expansion of this hyperoceanic biome has previously been explained as a consequence of Neolithic forest clearance. However, the present distribution of blanket bog in Great Britain can be predicted accurately with a simple model (PeatStash) based on summer temperature and moisture index thresholds, and the same model correctly predicts the highly disjunct distribution of blanket bog worldwide. This finding suggests that climate, rather than land-use history, controls blanket-bog distribution in the UK and everywhere else.

We set out to test this hypothesis for blanket bogs in the UK using bioclimate envelope modelling compared with a database of peat initiation age estimates. We used both pollen-based reconstructions and climate model simulations of climate changes between the mid-Holocene (6000 yr BP, 6 ka) and modern climate to drive PeatStash and predict areas of blanket bog. We compiled data on the timing of blanket-bog initiation, based on 228 age determinations at sites where peat directly overlies mineral soil. The model predicts large areas of northern Britain would have had blanket bog by 6000 yr BP, and the area suitable for peat growth extended to the south after this time. A similar pattern is shown by the basal peat ages and new blanket bog appeared over a larger area during the late Holocene, the greatest expansion being in Ireland, Wales and southwest England, as the model predicts. The expansion was driven by a summer cooling of about 2°C, shown by both pollen-based reconstructions and climate models. The data show early Holocene (pre-

Neolithic) blanket-bog initiation at over half of the sites in the core areas of Scotland, and northern England.

The temporal patterns and concurrence of the bioclimate model predictions and initiation data suggest that climate change provides a parsimonious explanation for the early Holocene distribution and later expansion of blanket bogs in the UK, and it is not necessary to invoke anthropogenic activity as a driver of this major landscape change.

1. Introduction

Blanket bog is a distinctive type of peatland confined to areas with cool and extremely wet climates. The name derives from the fact that the peat covers sloping ground and hilltops, as well as basins, thus 'blanketing' the landscape. Blanket bogs are widespread in the west and north of the UK (Great Britain and Northern Ireland) and occupy about 6 % of its land area (Jones et al., 2003). They are locally important (under various names) in other hyperoceanic regions of the world, although in total they cover only about 0.1% of the Earth's land surface (Gallego-Sala and Prentice, 2013).

The global distribution of blanket bogs today is confined to cool, wet climates (Gallego-Sala and Prentice, 2013). The initiation of blanket bog formation during the Holocene is regionally asynchronous, and in most regional has been found to coincide with a shift towards cooler, wetter climates (Zaretskia et al., 2001, Dirksen et al, 2012). However, there has been considerable debate about the cause of Holocene blanket-bog initiation in the UK.

There is a long-standing hypothesis, first proposed by Moore (1973), that it was a consequence of land use by Neolithic human populations, and in particular land clearing practices at the time of the 'elm decline' (often taken as a stratigraphic marker of Neolithic land use (Parker et al., 2002), as well as heavy stock grazing that changed the soil hydrological balance enough to initiate the inception of blanket bogs between about 6000 and 5000 yr BP (Moore, 1975; Moore, 1993; Merryfield and Moore, 1974; Robinson and Dickson, 1988; Huang, 2002). Evidence of removal of the shrub and/or tree cover by fire at the onset of blanket bog formation, and

pollen analytical studies suggesting intensive agricultural practices by Neolithic people support this hypothesis (Merryfield and Moore, 1974; Smith and Cloutman, 1988; Robinson and Dickson, 1988; Simmons and Innes, 1988). A recent investigation of initiation of upland blanket bogs in Ireland also pointed to land use as a principal cause of paludification (Huang, 2002). However, a number of authors have suggested the initiation of blanket bogs at specific locations solely as a result of a climatic shift during the mid Holocene 'Atlantic' period in Scotland (Ellis and Tallis, 2000; Charman, 1992; Tipping, 2008) the Faroe Islands (Lawson et al., 2007), and Ireland (Mitchell and Conboy, 1993; Dwyer and Mitchell, 1997). Tipping (2008) suggested that farming communities only settled in the Scottish Highlands after the landscape had already been covered by blanket bogs. Other authors have adopted a more complex view in which both climatic shifts and human activities played a role (Smith, 1970; Keatinge and Dickson, 1979; Tallis, 1991). Soil-forming processes, including leaching of base cations and consequent acidification and podsolization of soils, were also proposed to have been influential (Bennett et al., 1992; Charman, 1992; Smith and Green, 1995), giving rise to the term "pedogenic peats" (Simmons and Innes, 1988).

It is difficult to resolve such arguments about causality on the basis of timing alone. Lack of coincidence could be due to idiosyncratic local factors while synchronicity could arise by chance or because both events result from a common underlying cause. Under these circumstances, process-based modelling can offer a way forward. Globally, blanket bogs occur where the mean annual temperature (MAT) $> -1^{\circ}\text{C}$, the mean temperature of the warmest month (MTWA) $< 14.5^{\circ}\text{C}$ and the ratio of mean

annual precipitation to equilibrium evapotranspiration (moisture index, MI) > 2.1 (Gallego-Sala and Prentice, 2013). These limits ensure that the site is outside the permafrost zone and therefore not subject to cryoturbation, that summer temperatures are not too high for *Sphagnum* growth, and that there is sufficient moisture throughout the year to sustain peat growth on sloping ground. These limits have been used to construct a simple bioclimatic model, PeatStash (Gallego-Sala et al., 2010). In addition to predicting accurately the present-day distribution of blanket bog in Great Britain, PeatStash correctly predicts the highly disjunct global distribution of blanket bogs (Gallego-Sala and Prentice, 2013), including its occurrence in places such as Newfoundland and Kamchatka that have experienced very different land-use histories from the British Isles. This finding strongly suggests that the present-day distribution, at least, of blanket bogs everywhere is controlled by climate. If so, it is natural to hypothesize that climate change was responsible for the Holocene expansion of blanket bogs.

Here we use PeatStash to simulate the UK distribution of blanket bogs in the mid-Holocene (6000 years ago, 6 ka). We compare these simulations with a new compilation of blanket-bog initiation dates, in order to explore whether climate change could plausibly account for the expansion of blanket bogs during the later Holocene.

2. Methods

We predicted the distribution of blanket bog at 6 ka using PeatStash (Gallego-Sala et al., 2011) with climate inputs derived from (a) climate model simulations of the 6 ka

climate and (b) pollen-based climate reconstructions. The climate models provide predictions of a mutually consistent set of meteorological variables; using multiple climate models allows us to encompass the uncertainty resulting from differences between models. The climate models were run at relatively coarse resolution (Table 1) and there may be systematic biases that afflict all of the models (Harrison et al., 2013). Pollen-based reconstructions provide an independent source of information. However, their distribution is not continuous across the whole of the UK and the necessity to interpolate between reconstructions at individual sites could introduce uncertainty (Bartlein et al., 2011). Nevertheless, this information provides a useful check of the reliability of the simulated climates at the location of the sites and an alternative scenario of climate change. We therefore used both the climate-model ensemble and the pollen-based reconstructions to obtain mid-Holocene climate estimates to drive PeatStash. We then compared the PeatStash projections with a new compilation of data on the timing of blanket-bog initiation in the UK.

2.1 The PeatStash Model

PeatStash simulates the potential distribution of blanket bog (Gallego-Sala et al., 2010) based on mean annual temperature (MAT), mean temperature of the warmest month (MTWA) and a moisture index (MI) calculated from long-term monthly means of temperature, precipitation, and fractional sunshine hours. The definition of MI follows UNEP (United Nations Environment Programme, 1992):

$$MI = P / PET$$

(1)

where P is the mean annual precipitation (mm) and PET is the mean annual potential evapotranspiration (mm). We substitute equilibrium evapotranspiration (E_q), calculated from monthly net radiation and temperature, for PET in equation (1). E_q is given by $\lambda E_q = [s/(s + \gamma)]R_n$ where λ is the latent heat of vaporization of water, s is the slope of the Clausius-Clapeyron relationship, γ is the psychrometer constant and R_n is net radiation, calculated from latitude, season and fractional sunshine hours. The use of E_q instead of PET affects only the absolute magnitude of MI , because PET as computed by the Priestley-Taylor equation is directly proportional to E_q . PeatStash requires $MI > 2.1$, $MAT > -1^\circ\text{C}$ and $MTWA < 14.5^\circ\text{C}$ to determine the presence of blanket bog.

The model predicts the distribution of blanket bog in Great Britain with reasonably high accuracy (Figure 1; Gallego-Sala et al., 2010). Detailed comparison for Northern Ireland was not possible because of the lack of accurate high-resolution data on blanket-bog distribution. However, comparisons with published maps suggest that the broadscale patterns are also captured there (Gallego-Sala and Prentice, 2013).

2.2 Simulated climate data

We used output from ten climate models (Table 1) that had performed Mid-Holocene (6 ka) and pre-industrial (PI) simulations as part of the Coupled Modelling Intercomparison Project (CMIP5). The 6 ka simulations were driven by appropriate changes in insolation and greenhouse gas concentrations (Taylor et al., 2011). Anomalies (6 ka minus PI) of precipitation, temperature and fractional sunshine hours were bi-linearly interpolated from the original model grid to a common 0.5° grid. These anomalies were then added to

a baseline modern climate, derived from the CRU CL2.0 long-term mean climatology (temperature, precipitation, fractional sunshine hours) for the period 1931-1960 (New et al., 2000).

2.3 Pollen-based climate reconstruction

We used reconstructions of MAT, MTWA, mean annual precipitation (MAP) and α (the ratio of actual to equilibrium evapotranspiration, calculated as in (Cramer and Prentice, 1988) from the Bartlein et al. (2011) data set. Bartlein et al. (2011) provided a harmonized compilation of pollen-based climate reconstructions, where individual site-based reconstructions were aggregated to provide estimates of mean conditions (with their uncertainties) on a 2° x 2° grid. Anomalies of each climate variable were interpolated from the original resolution grid to the 10 x 10 km grid of the UKCIP_02 baseline climatology (<http://www.cru.uea.ac.uk>). We do not account for reconstruction uncertainties in this application because they are smaller than the differences between the climate-model scenarios.

PeatStash was run using MAT and MTWA as direct inputs, while MI was calculated from MAP and α . Assessed over a period of years, α can be related to MI using the Budyko hydrological relationship, which can be expressed as follows (Wang et al., 2012; Zhang et al., 2004):

$$\alpha = 1 + m - (1 + m^w)^{1/w}.$$

(2)

where $m = \text{MI}$ and w is a parameter. To estimate anomalies of MI (Δm) from anomalies of α ($\Delta\alpha$), we set $w = 3$ (Zhang et al., 2004), take the derivative of equation (2) and apply the approximation $\Delta\alpha \approx \Delta m (\partial\alpha/\partial m)$, where:

$$\partial\alpha/\partial m = 1 - [m/(1 + m^w)^{1/w}]^{w-1}.$$

(3)

2.4 PeatStash 6 ka simulations

We ran PeatStash using output from each of the ten climate models. Given model-dependent differences in the simulated climates (Harrison et al., 2013), the ensemble of simulations is used to provide an estimate of the probability that suitable climates for blanket bog existed by 6 ka in specific regions based on the consistency between the ten projections. PeatStash simulations were also driven by pollen-based climate reconstructions of climate anomalies, which were superimposed on the higher-resolution UKCIP grid.

We present the results of the 6 ka PeatStash simulations as anomalies from present. Wherever blanket bog is simulated for 6 ka, we predict that climate conditions were suitable for early initiation. Where blanket bog is simulated for PI but not for 6 ka, we predict that blanket bog initiation occurred after 6 ka. Where blanket bog is simulated for 6 ka but not for PI, we predict that conditions became unsuitable for blanket bog growth after 6 ka.

2.5 Basal Age Dataset

We assembled basal radiocarbon dates from blanket bogs throughout Great Britain

and northern Ireland. We adopted a stringent exclusion criterion, accepting only sites where blanket-bog formation commenced directly over mineral parent material and not as a change from a minerotrophic peatland (i.e. we have only included ombrogenous peatlands). We recorded the different topographic positions (saddle, bottom of the valley, slope, top) and altitudes of each site, whenever possible. The dataset includes 64 records of pollen-analytically determined dates of peat initiation based on regional correlation of dated pollen-stratigraphic events. The remaining 164 records have either been directly dated from basal peat deposits, or there were sufficient radiocarbon dates to develop an age-depth model allowing the basal age to be well constrained. The extrapolated dates may provide more accurate estimates of basal ages than radiocarbon assays of basal peats, which often yield young ages because of contamination by mobile humic acids and root penetration (Smith and Cloutman, 1988; Charman, 1992). Any errors associated with the age modelling are expected to be considerably less than the 1000-year windows used in mapping peatland changes in our analyses. A total of 228 basal age estimates (see Supplementary Information) were assembled but the full data complement was not available for all of these.

There is a difference between peat initiation and peat spread, and the latter cannot strictly be inferred from a single sampled point. There is local variability in peat initiation depending on topographic position, slope gradient, and altitude (Charman, 1992) and so a single sampled site may not capture the oldest peat initiation date. Blanket bog does not necessarily grow by uniform spread of peat but probably coalesces from different foci (Tipping, 1994). Furthermore, we are reliant on

published and unpublished data collected for a variety of reasons that may have biased sampling towards deeper or shallower locations. Despite these known limitations in using basal dates to infer initiation, these effects will be similar for all regions and our data set is sufficiently large and regionally comprehensive to provide information on the patterns of peat initiation in different regions.

3. Results and Discussion

The climate-model simulations consistently show summers warmer than today's over most of northern Europe. Mean annual precipitation (MAP) was slightly reduced in northern Britain and slightly increased in southern Britain compared to today. Conditions suitable for blanket bog are predicted at 6 ka across much of Scotland and northern England (Figure 2a), but warmer than present summers restricted blanket-bog distribution in southwest Scotland, Northern Ireland and Wales. Southwest England was almost entirely unsuitable for blanket-bog formation at 6 ka, at least at the spatial resolution of the model grid, but became more suitable for blanket-bog development after the mid-Holocene.

The suitability of different regions for blanket bog is examined in more detail using the high-resolution PeatStash simulations driven by quantitative palaeoclimate reconstructions. The pollen-based reconstructions (Bartlein et al., 2011) confirm that the climate over the British Isles was slightly wetter at 6 ka than today (Figure 3), with considerably warmer (approximately 2°C) summers. As a result of the warmer summers, the bioclimatic envelope suitable for blanket bog was 14 % smaller at 6 ka (Figure 2b). Larger areas of western Scotland, Ireland and Wales

have become suitable for blanket bog since 6 ka. Southwest England acquired three separate centres of predicted peat growth, corresponding to Dartmoor, Exmoor and Bodmin Moor, as a direct consequence of late Holocene cooling.

These simulations are consistent with observations of regional timing in the formation of blanket bogs (Figure 4a). Analysis of basal dates on blanket bogs shows a gradual increase in blanket-bog formation throughout the early Holocene and a broad peak in initiation dates between 8000 and 4000 BP during the mid-Holocene. There is a decline in the number of ages after 3-4000 BP. Regional patterns suggest that initiation occurred earliest in the north and most of the dates between 10000 and 7000 BP are from sites in Scotland and northern England (Figure 4a). Sites in Wales also have some early ages, but with a major increase in initiation dates after 8000 BP continuing throughout the rest of the Holocene. Sites in Ireland and southwest England are generally later to develop and have a peak at 3000 BP, later than the other regions. The initiation dates show that large areas of northern Britain were climatically suitable for blanket-bog formation before 6 ka, and remain so now. The regional differences in timing of initiation indicate a gradual increase in the area with suitable climate after 6 ka, especially in Wales, Ireland and southwest England. There are some discrepancies between the simulated and observed patterns of blanket-bog growth. Most of the exceptions are occurrences of initiation dates > 6 ka in areas such as Dartmoor that are only predicted to become suitable for peat growth after 6 ka. This may be an issue of resolution; some blanket bogs may have developed in localities with suitable microclimates that are smaller than our model can resolve, given the resolution of the climate inputs. It is also possible that this

reflects a sampling bias. Older locations tend to be over-sampled because deep peat deposits are generally favoured in order to generate longer palaeorecords (Fyfe and Woodbridge, 2012). These may not have been laterally extensive or typical of the wider landscape.

We model a slight contraction in the area of suitable climate for blanket bog since 6 ka in eastern Britain (Figure 2). If this model result is correct, there should be areas of eastern Britain supporting relict blanket bog with no active peat formation. Although peat initiation occurred in these areas between 4 and 2 ka (Figure 4a), post-6 ka accumulation rates are low (Simmons and Innes, 1988) suggesting that conditions indeed became less favourable for peat growth. Peat growth may continue for some time on an established peat bog due to local edaphic and hydrological conditions, despite climate being unsuitable for peat initiation. The existence of relict peats is not susceptible to testing using only initiation dates and this prediction would need to be explicitly tested by field sampling for cessation or slowing of peat growth.

Our analysis of basal peat ages shows that blanket bogs have been developing in some regions of the British Isles from the early Holocene onwards. The fact that blanket bogs developed later in the west and south of the country can be explained simply by the fact that regions with warmer and/or drier climates (Figure 3) were less suitable for peat formation during the early Holocene. Blanket bogs only developed in these areas as climate became cooler and wetter. Blanket-bog formation accelerated in the mid- to late Holocene, but this occurred later than the 'elm decline' event in many locations and proceeded continuously, which makes it

unlikely that it was causally linked to human activities. The simulations (Figure 2) indicate that a large part of the British Isles was suitable for blanket-bog formation before the main period of human impact.

Climatic control of blanket-bog formation in the UK is consistent with evidence from other parts of the world that blanket-bog initiation occurred in response to climate change and that their current distribution is strongly controlled by climatic conditions. It raises an important issue about the fate of this unique ecosystem under future climate change. Our work supports previous analyses that suggest they will require careful management given that their continued growth may be threatened by large-scale shifts in climate in some regions of the UK (Clark et al., 2010; House et al., 2010; Gallego-Sala et al., 2010) and worldwide (Gallego-Sala and Prentice, 2013).

Taken together, these lines of evidence indicate that the history of blanket-bog growth in the British Isles can be explained as a threshold response to a changing climate. In an area with a rich human history, such as the British Isles, almost all Holocene palaeoecological records show signs of human impact at various stages. However, our analyses suggest that no human intervention was required to initiate blanket-bog formation in the British Isles.

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AG-S, ICP and DC contributed to the conception of the paper, GL and SPH provided input to the climate-model analyses; all authors contributed to the analyses and writing of the paper.

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Figure and Table Captions

Figure 1. The area of blanket peat predicted by the bioclimatic envelope model (BCEM) PeatStash using a baseline climate period (UKCIP02: 1961-90) overlain on the mapped 5 km gridded data of observed blanket peat presence (Ordnance Survey/EDINA, 2009).

Figure 2. PeatStash simulations of blanket peat extent at 6 ka using a) simulated palaeoclimate and b) pollen-based reconstructions of palaeoclimate.

Figure 3. Average climate anomalies at 6 ka from pollen-based reconstruction: a) moisture index, b) mean annual temperature (MAT), and c) temperature of the warmest month (MTWA).

Figure 4. Assembled basal calibrated radiocarbon dates from blanket bogs over the British Isles: a) regional graphs of initiation dates through time binned every 500 years; b) map of individual initiation dates; and c) map of initiation dates summarised per region.

Table 1. Summary information on the climate models used in this analysis.

Table 2: Region by region break down of percentage of a) cores with basal dates younger than 6ka b) sites with basal dates exclusively younger than 6ka c) %

gridcells that PeatStash predicts to have initiated after 6ka when run with the pollen-based climate reconstructions.

Table 1. Summary information on the climate models used in this analysis.

Model name	Type	Model components	Atmospheric Resolution (no of gridcells: lat, lon)	Reference
CCSM4	OA	CAM4/POP2/CLM4/CICE4/CPL7	192, 288	(Gent et al., 2011)
CNRM-CM5	OA	ARPEGE-Climat V5.2.1, TL127L31/NEMO3.3.v10.6.6P/ORCA1degL42)/ GELATOV5.30/TRIPv1/SURFEXv5.1.c/OASIS 3	128, 256	(Voldoire et al., 2013)
CSIRO-Mk3-6-0	OA	AGCMv7.3.5/GFDL MOM 2.2	96, 192	Rotstayn et al. (2010)
MPI-ESM-P	OA	ECHAM6/MPIOM	96, 192	Giorgetta et al. (2013)
MRI-CGCM3	OA	GSMUV/MRI.COM3/ HALv0.31	160, 320	Yukimoto et al. (2011)
BCC-CSM1-1	OAC	BCC_AVIM1.0/MOM4/ SIS	64, 128	Wu et al. (2013)
IPSL-CM5A-LR	OAC	LMDZ4_v5/ORCA2(NEMOV2_3)/ LIM2(NEMOV2_3) /PISCES/ORCHIDEEE	96, 96	Dufresne et al. (2013)
MIROC-ESM	OAC	MIROC-AGCM (2010)/COCO3.4/SPRINTARS 5.00/NPZD/SEIB-DGVM	64, 128	Watanabe et al. (2011)
HadGEM2-CC	OAC	HadGAM2/HadGOM2/TRIFFID/diat-HadOCC	145, 192	Collins et al. (2011)
HadGEM2-ES	OAC	HadGAM2/HadGOM2/MOSES2/TRIFFID/UKCA/diat- HadOCC	145, 192	Collins et al. (2011)

Table 2: Region by region break down of percentage of a) cores with basal dates younger than 6ka b) sites with basal dates exclusively younger than 6ka c) % gridcells that PeatStash predicts to have initiated after 6ka when run with the pollen-based climate reconstructions.

Region	% cores with basal date <6ka	%sites with basal date exclusively <6ka	% gridcells with basal date <6ka
N Scotland	54	35	24
C Scotland	18	20	31
S Scotland	17	33	41
N England	28	32	38
Wales	20	48	64
N Ireland	93	93	42
SW England	73	38	95
All	44	43	48