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Key Points:

- Climate signal preservation in peat determined by both magnitude and rate of climate change
- Ecohydrological feedbacks in bogs provide high- and low-pass filters for climatic signals
- Timing of peat humification signals consistently offset from climatic drivers

Supporting Information:

- Text S1 and Figures S1–S5
- Table S1
- Software S1
- Software S2

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Untangling climate signals from autogenic changes in long-term peatland development

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Abstract Peatlands represent important archives of Holocene paleoclimatic information. However, autogenic processes may disconnect peatland hydrological behavior from climate and overwrite climatic signals in peat records. We use a simulation model of peatland development driven by a range of Holocene climate reconstructions to investigate climate signal preservation in peat records. Simulated water-table depths and peat decomposition profiles exhibit homeostatic recovery from prescribed changes in rainfall, whereas changes in temperature cause lasting alterations to peatland structure and function. Autogenic ecohydrological feedbacks provide both high- and low-pass filters for climatic information, particularly rainfall. Large-magnitude climatic changes of an intermediate temporal scale (i.e., multidecadal to centennial) are most readily preserved in our simulated peat records. Simulated decomposition signals are offset from the climatic changes that generate them due to a phenomenon known as secondary decomposition. Our study provides the mechanistic foundations for a framework to separate climatic and autogenic signals in peat records.

1. Introduction

1.1. Background

Peatlands represent important archives of Holocene paleoclimatic change, particularly in mid and high latitudes of the Northern Hemisphere [e.g., *Booth and Jackson*, 2003; *Charman et al.*, 2006; *Swindles et al.*, 2013]. Peat-based climate reconstructions from ombrotrophic (rain-fed) bogs rely on the assumption that downcore trends in humification (degree of decomposition), plant macrofossil assemblages, and testate amoeba-based reconstructions of water-table depths are related to past climatic forcing. *Charman* [2007] proposed that reconstructions of bog surface wetness should be interpreted primarily as records of growing season water deficit (precipitation minus evapotranspiration), although a debate exists over the relative roles of temperature and rainfall in driving hydrological changes in bogs [e.g., *Barber and Langdon*, 2007; *Barber et al.*, 2000; *Charman et al.*, 2004, 2009].

A complex network of ecosystem-scale feedbacks [e.g., *Belyea*, 2009; *Waddington et al.*, 2015] means that peatland ecohydrological processes may be governed at times by autogenic, rather than climatic, influences. *Swindles et al.* [2012] demonstrated how a simple but plausible set of ecohydrological feedbacks could lead to homeostatic recoveries in bog water tables after abrupt climate shifts. Slow (i.e., millennial-scale) climatic changes may be particularly vulnerable to signal overwriting by internal processes, prompting some researchers to filter low-frequency information out of peat-based climate reconstructions [e.g., *Charman et al.*, 2006]. *Aaby* [1976] and *Barber* [1981] both proposed that under a stable climate the continued accumulation of peat could cause a bog surface to rise more rapidly than the water table, leading to spontaneous surface drying and pool infilling. The possibility of spontaneous drying has led some researchers to omit dry markers in peat sequences from subsequent reconstructions [e.g., *Barber et al.*, 1994; *Mauquoy and Barber*, 1999], although more recent work [e.g., *Booth et al.*, 2006; *Clifford and Booth*, 2013; *Swindles et al.*, 2010] has presented strong evidence for peat-based preservation of multicentennial phases characterised by intense droughts. Given the apparent possibility for autogenic changes in peatlands through multiple mechanisms, it is unclear how to untangle climate signatures in peat records from those related to internal processes. *Charman* [2007] concluded that simulation models of peat accumulation and hydrological processes are required in order to understand the complex, nonlinear responses of peatlands to long-term climatic forcing and to separate the respective influences of temperature and rainfall.

Signal preservation in peat records also seems likely to vary between proxies. Humification represents a time-integrated record of peat decomposition and may therefore be vulnerable to signal overwriting

[*Borgmark and Schoning*, 2005; *Payne and Blackford*, 2008; *Tipping*, 1995], whereas testate amoeba and plant macrofossil assemblages are thought to provide more of a snapshot of environmental conditions from when a peat layer was formed [e.g., *Amesbury et al*., 2010].

A number of abrupt, large-magnitude, geographically extensive climatic events are clearly identifiable in peat records. Examples include the cool, wet 2.7 ka B.P. event in NW Europe [*Swindles et al*., 2013] and multicentennial drought episodes in North America [*Booth et al*., 2006; *Clifford and Booth*, 2013]. However, peat-based evidence for some suspected events is ambiguous or inconsistent between reconstructions from different regions [e.g., *Booth et al*., 2005; *Roland et al*., 2014]. Such inconsistencies seem likely to reflect some combination of (i) genuine regional differences in climate [*Roland et al*., 2014], (ii) the role of autogenic processes in determining peatland sensitivity to climate forcing [*Aaby*, 1976; *Barber*, 1981; *Swindles et al*., 2012; *Waddington et al*., 2015], and (iii) subsequent modification, removal, and overwriting of climate information in peat records by autogenic processes [*Borgmark and Schoning*, 2005; *Tipping*, 1995].

1.2. Aim and Research Questions

Here we explore the relative roles of climate and autogenic mechanisms in governing peatland developmental dynamics. We address the following specific questions:

1. What modes and magnitudes of climatic change are likely to have the greatest effect on bog development?
2. What climatic conditions and stages of bog development, if any, leave peat records vulnerable to overwriting by autogenic processes after peat formation?
3. What level of detail of information about Holocene climate change should we expect to be able to recover from peat records of decomposition and water-table depth?

Our questions lend themselves naturally to a simulation modeling approach, which affords a degree of control rarely achievable in observational studies [cf. *Charman*, 2007]. Because the climate used to drive a peatland development model is specified—and therefore known exactly—the model's response to climatic events can be evaluated with certainty.

2. Method

2.1. Model Description

We used an extensively modified one-dimensional version of the DigiBog model to simulate 8000 years of peatland development and response to Holocene climate change. The new model is described in full in Text S1 in the supporting information, but major changes to previously published versions [e.g., *Morris et al*., 2011; *Swindles et al*., 2012] include temperature dependency of (i) litter production (i.e., plant productivity), (ii) peat decomposition (we used a Q_{10} function), and (iii) evapotranspiration (and so net rainfall).

During each annual time step the model simulates (i) the formation of fresh peat at the top of a simulated soil column, at a rate determined by annual air temperature and simulated water-table depth; (ii) decomposition of old peat, again at a rate determined by temperature and water table, as well as the degree of decomposition (well-decomposed peat is biochemically more recalcitrant and so decomposes more slowly than fresh, labile peat); (iii) water-table behavior based on precipitation, evapotranspiration, and shallow drainage through the peat; and (iv) changes in peat hydraulic conductivity due to decomposition. Model outputs include time series of water-table depth, peat thickness, and transmissivity (the depth integral of hydraulic conductivity below the water table). Final depth profiles of simulated peat properties (e.g., degree of decomposition) at the end of an 8000 year simulation may be thought of as model equivalents of coring a real bog. Although our model is necessarily a simplified representation of reality (all models are), it represents key processes and feedbacks that are influential in peatland development and climate signal preservation. The model's equations and parameter values are also informed by extensive measurements and a partial sensitivity analysis (Text S1).

We based our simulations broadly on Malham Tarn Moss, a raised bog in northern England (54.098°N, 2.173°W; 380 m above sea level; see Text S1 for full site description). Doing so enabled comparisons with our previous modeling work [*Swindles et al*., 2012] and also allowed a partial validation of the model by ensuring that broad predictions such as water-table depth variations and long-term rates of peat accumulation were within plausible

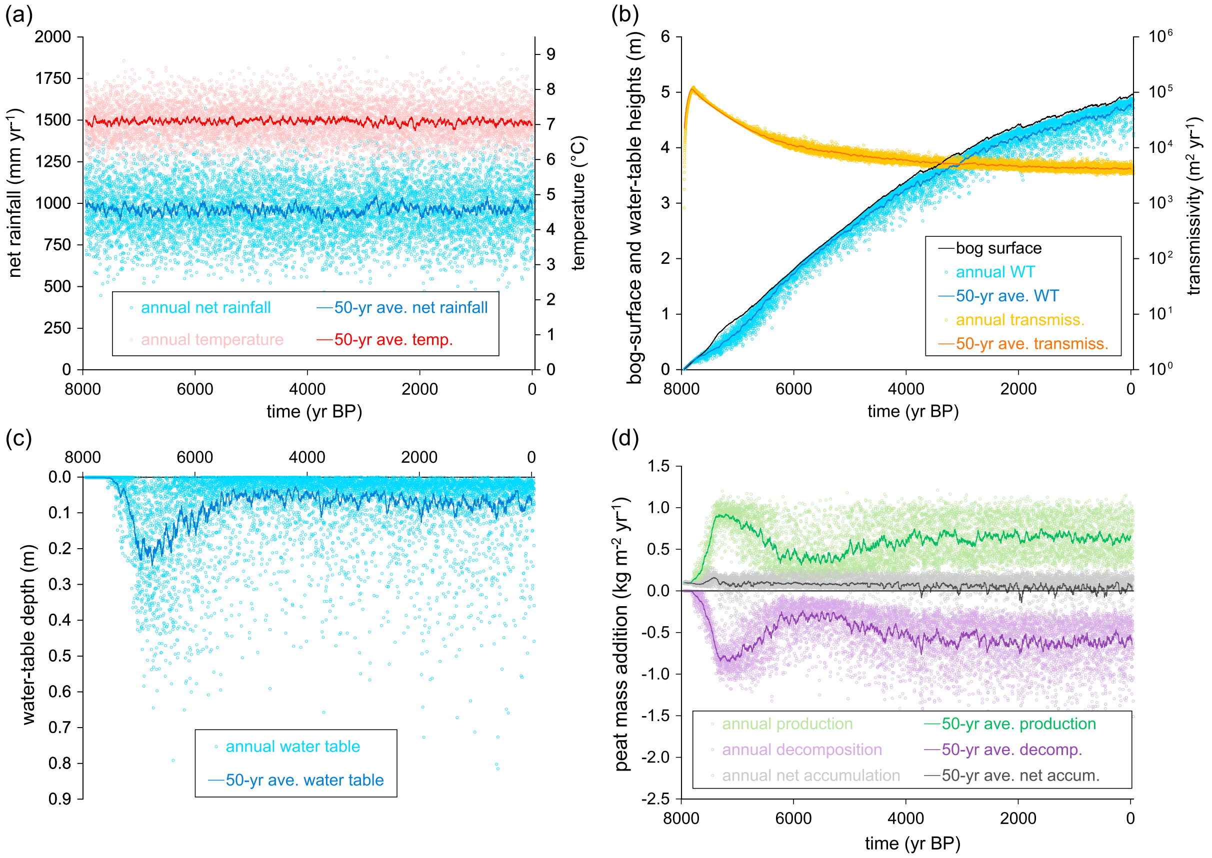

Figure 1. Time series of simulated bog development under the constant "baseline" climate. Net rainfall (a) is total precipitation minus evapotranspiration. Transmissivity (b) is the depth integral of hydraulic conductivity below the water table (dimensions of $L^2\ T^{-1}$) and is important to determining rates of water loss through lateral drainage. Note the autogenic drying followed by wetting during early stages of bog development (c) despite constant climate drivers.

ranges for the site. However, our aim was to understand in general terms those ecohydrological mechanisms that determine the degree of connection between external climatic drivers and internal peatland dynamics, not to simulate a specific site in close detail. We did not undertake a parameter tuning exercise nor a full validation of the model's outputs against peat stratigraphy or water-table reconstructions from the site.

2.2. Experimental Design and Driving Data

We performed two sets of simulations with the updated version of DigiBog. We drove the first set of simulations using a synthetic climate data set that includes noisy interannual variability but no long-term trends (Figure 1a). We used the Long Ashton Research Station Weather Generator (LARS-WG) [*Semenov and Barrow*, 1997] to produce 8000 year series of annual temperature and net rainfall (precipitation minus evapotranspiration) data based on observed variability at Malham Tarn. Interseries correlation, temporal autocorrelation, and constant long-term means (7.1°C and 970 mm yr^{-1}) were calculated from instrumental data for the study site (1961–2000 Common Era) (UK Met Office, unpublished data; enquiries@metoffice.gov.uk). Although not a realistic representation of the Holocene, holding long-term climatic averages constant in this way enabled a high level of experimental control by providing a baseline simulation against which to compare the effects of simulated climatic excursions. To this end we then superimposed a variety of synthetic ramp increases and decreases onto the baseline rainfall and temperature series (Figures 2 and 3).

In a second set of simulations we drove the model using a more realistic reconstruction of Holocene climate for the study site since 7.95 ka B.P. (Figure 4; and Figure S5 in the supporting information). We based our representation of Holocene climate on a combination of recent instrumental data and a variety of existing multiproxy reconstructions [*Luterbacher et al.*, 2004; *Mauri et al.*, 2015; *Pauling et al.*, 2006; *Xoplaki et al.*, 2005] downscaled for our site. We also superimposed cool, wet spike signals onto the noisy temperature and rainfall series to

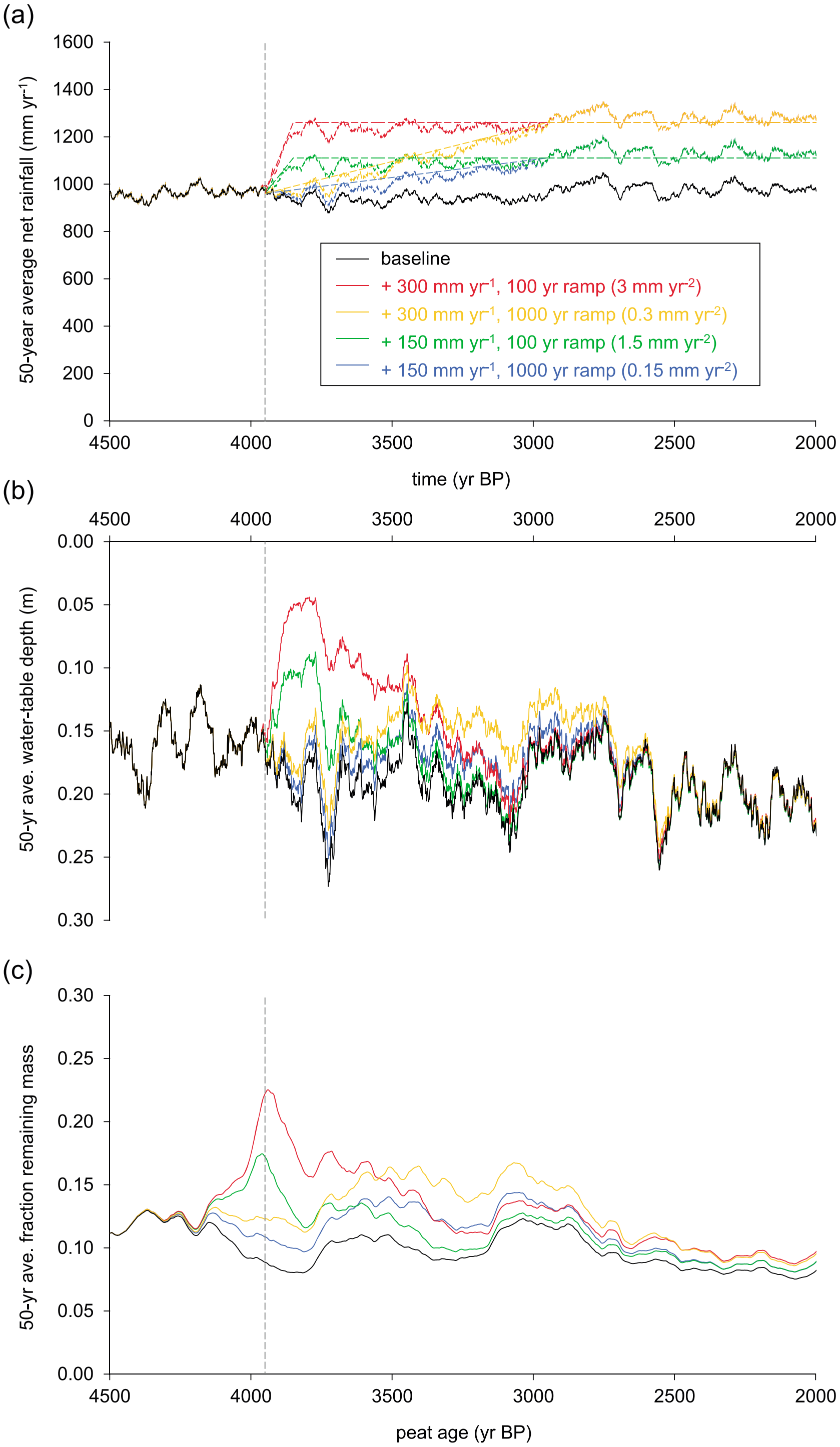

Figure 2. Response of simulated water tables (b) and final decomposition profile (c) to ramp increases (broken line time series) in rainfall superimposed onto constant baseline climate (a). In all cases the prescribed climate shifts begin at 3950 ka B.P. (indicated by broken vertical lines). Series names in legend indicate the magnitude of the rainfall shift, the length of time the climate ramps were applied for, and the resultant rate of change of rainfall (hence units of mm yr^{-2}). All values displayed as 50 year running means to highlight trends; consult Figure 1 for an indication of interannual variability in the respective time series. Fractional remaining mass (Figure 2c) is a measure of degree of decomposition in a virtual peat core at the end of an 8000 year simulation; values close to 1 indicate fresh, poorly decomposed peat; values close to zero indicate heavily decomposed peat.

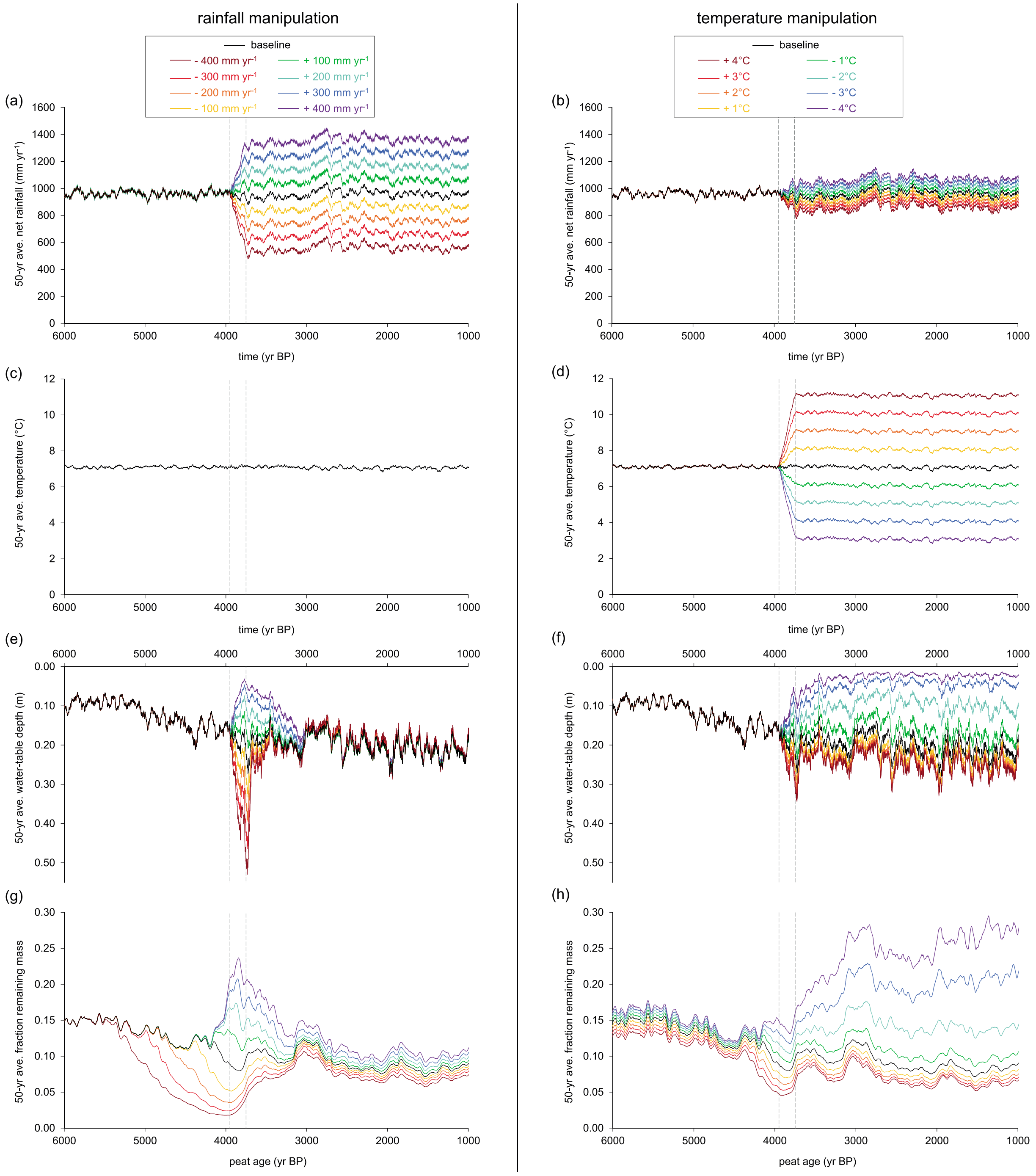

Figure 3. Response of simulated bog to ramp changes in rainfall (left-hand side) compared to ramp changes in temperature (right-hand side). Changes in temperature (d) necessarily also cause changes in net rainfall (b) due to changes in evapotranspiration, although the effect is smaller than the independent manipulation of rainfall (a). Broken vertical lines indicate beginning and end of prescribed climate ramps (200 year duration in all cases).

represent the 4.2 and 2.7 ka B.P. events. Unlike in the first set of simulations where we manipulated either temperature or rainfall in isolation, our representations of the 4.2 and 2.7 ka B.P. events here comprised simultaneous spikes in both rainfall and temperature. Although the chronologies of these climatic excursions are well constrained [*Drysdale et al.*, 2006; *Martin-Puertas et al.*, 2012; *Plunkett and Swindles*, 2008; *Roland et al.*, 2014], their magnitudes are contested, so we experimented with the size of the spikes used to represent them. See Text S1 for full method.

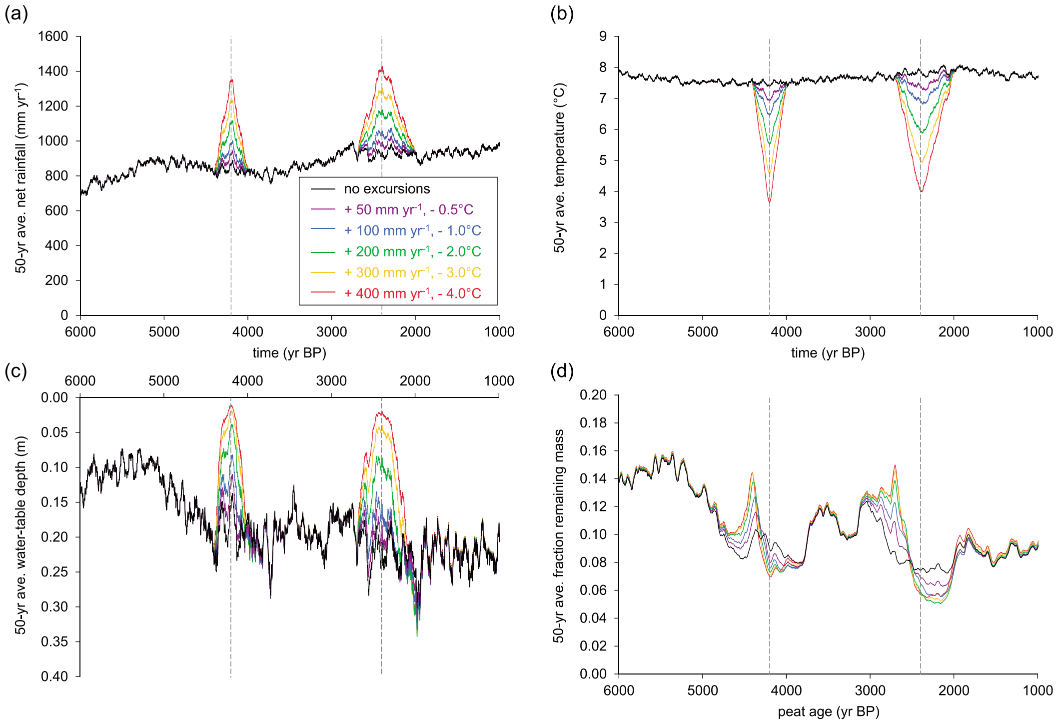

Figure 4. Simulated bog development and response to climatic shifts (c and d) when driven by Holocene climate reconstruction (a and b). Unlike in Figures 1 to 3 where temperature or rainfall was manipulated in isolation, our representations of the 4.2 and 2.7 ka B.P. events here comprise simultaneous spikes in both rainfall and temperature. Series names in legend indicate magnitudes of the 4.2 and 2.7 ka B.P. events at their peak intensities (timings of peak intensities indicated by broken vertical lines). See Figure S5 for the entire 8000 year climate reconstruction, including interannual variability.

3. Results and Discussion

The strengths of rainfall signals in simulated water-table behavior and final decomposition profiles were governed by not only the magnitude but also the rate of change of climate. Rapid, large-magnitude changes in rainfall created strong signals in both simulated water-table behavior and final peat decomposition profiles (e.g., rate of change of rainfall 3 mm yr^{-2}; Figure 2, red series). However, small-magnitude changes in rainfall still generated noticeable responses when they occurred rapidly (e.g., 1.5 mm yr^{-2}; Figure 2, green series). If changes in rainfall occur slowly, then even large-magnitude climate events have little effect on model behavior; the modest signal left in peat records by a slow change in rainfall is mainly lost against a background of annual to decadal noise and would be unlikely to be identified as a climatic event (e.g., 0.3 mm yr^{-2}; Figure 2, yellow series).

The model's governing equations combine to form stable attractors (values that the model tends toward under a given set of driving conditions and parameters) that moderate simulated water-table depth, peat accumulation regimes, and drainage [*Morris et al.*, 2012; see also *Belyea and Clymo*, 2001; *Hilbert et al.*, 2000]. When changes in rainfall occur slowly the homeostatic response of the simulated peatland is rapid enough that the system stays close to its water-table attractor. Slow changes in rainfall are thus largely absorbed by the simulated bog's negative feedbacks between peat accumulation, decomposition, changes in hydraulic properties, and drainage. More rapid changes in rainfall outpace this capacity for resistance, causing a noticeable spike in water tables (Figure 2b) and the final decomposition profile (Figure 2c). Through these mechanisms the simulated bog acts as a high-pass filter for rainfall signals, removing low-frequency information. We propose that even large-magnitude changes in rainfall may be filtered from peat records by internal processes if those rainfall changes occur slowly (i.e., millennial time scales), lending support to the hypothesis that slow changes in reconstructions of bog surface wetness may be unreliable climatic indicators [e.g., *Charman et al.*, 2006]. Additionally, this finding indicates that peatland development models driven with unrealistically rapid (i.e., instantaneous) step changes in future temperature or rainfall [e.g., *Ise et al.*, 2008] may paint an overly pessimistic picture of the vulnerability of peatland ecosystems and carbon stocks.

Our simulations provide only limited evidence for the hypotheses of *Aaby* [1976] and *Barber* [1981] that bogs can undergo spontaneous dry shifts under a constant climate. The baseline simulation with no long-term trends in climate showed a gradual, persistent deepening of the simulated water table throughout the majority of the 8000 year period (Figures 1c and 3f, black series). However, the rate of water-table change is so slow that it would be unlikely to be mistaken for a climatic trend in a paleohydrological reconstruction [cf. *Charman et al.*, 2006]. Additionally, all simulations exhibited a rapid autogenic deepening of the water table in the earliest stages of bog development, followed by a rapid autogenic shallowing (e.g., Figure 1c). This behavior is consistent with the hypothesis of *Hughes et al.* [2000] that bogs are less climatically sensitive immediately after ombrotrophication. During these early stages the entire nascent peat profile is poorly decomposed and is thus highly permeable [cf. *Grover and Baldock*, 2013; *Morris et al.*, 2015]. Rapid drainage means that bog surface rise initially outpaces water-table rise, leading to surface drying, increased productivity, and so increased peat accumulation rates (Figure 1d). Only once time-integrated decomposition causes transmissivity—and so drainage rates—to decline can the water-table mound begin to develop. We cautiously suggest that once a bog has become climate-sensitive, large, abrupt changes in water-table regime typically require an external forcing. This finding supports the use of dry markers in peat records as indicators of severe drought [e.g., *Booth et al.*, 2006; *Clifford and Booth*, 2013; *Swindles et al.*, 2010].

Resilient (i.e., homeostatic) autogenic behavior of the type demonstrated by *Swindles et al.* [2012] was much more apparent and occurred in all simulations with long-term changes in rainfall. Rainfall shifts of sufficient rate and magnitude serve to move the model's state variables (water-table depth, transmissivity, and degree of decomposition) away from their attractors. Negative feedbacks in the model then bring the simulated system back toward these attractors over a period of decades to centuries through changes in peat accumulation rates, hydraulic properties, and drainage. For this reason, step changes in rainfall tend to leave a spike in water-table and decomposition records, while a spike in rainfall tends to leave a spike followed by dip in simulated peat records (Figure 4d). While the onset of an abrupt water-table shift would seem to require climatic forcing, the subsequent ecohydrological behavior of a bog shortly after this initial shift may be dominated by autogenic mechanisms as the system recovers. Under a constantly varying climate, such homeostatic recoveries would be superimposed onto climatic signals throughout the peat record.

The model was much less resilient to changes in temperature than it was to rainfall. Ramp changes in long-term average temperature led to lasting changes in the water-table attractor. Large-magnitude (i.e., 3°C or 4°C) decreases in temperature over 200 years were sufficient to push the simulated bog from a predominantly dry status with water-table depths around 0.2 m to a wet status with water tables close to the surface (Figure 3f). The strong, lasting influence of temperature largely reflects reductions in litter production and so slow peat accumulation in colder temperatures. Changes in peat hydraulic structure, controlled by decomposition regimes, provide bog water tables with resilience to rainfall shifts via altered drainage rates, but the same mechanism is less relevant to temperature shifts. Our results suggest that changes in temperature may exert a more lasting influence over bog surface wetness than do changes in rainfall and may therefore be more readily preserved in peat records [cf. *Charman et al.*, 2009].

The model's algorithms have replicated a phenomenon known as secondary decomposition (in the sense of *Tipping* [1995]), whereby a deepening water table during a warm, dry period exposes relatively poorly decomposed peat deeper in the profile to enhanced oxic decomposition, where previously it had been well preserved by a shallower water table. Similarly, a shallowing water table in a cooling, wetting climate acts to preserve younger, near-surface peat layers that would otherwise have experienced rapid oxic decomposition [e.g., *Borgmark and Schoning*, 2005; *Tipping*, 1995]. These simple mechanisms give rise to a number of complex model behaviors, which we explore below.

Simulated water tables were highly sensitive to high-frequency (e.g., annual) variations in rainfall and temperature and responded readily to climatic drivers at these short temporal scales (Figures 2b, 3e, and 3f). However, these high-frequency fluctuations are not preserved in the peat decomposition profile at the end of an 8000 year simulation (Figures 2c, 3g, and 3h). The overall effect of repeated high-frequency water table fluctuations is to smooth the decomposition record, filtering out high-frequency information. The persistent action of secondary decomposition therefore acts as a low-pass filter for climatic signals. The combination of high-pass (from ecohydrological feedbacks) and low-pass (from secondary decomposition) filters suggests that rainfall variations of an intermediate frequency (multidecadal to centennial) are likely to be most readily recoverable from peat-based reconstructions.

Secondary decomposition also causes a systematic bias in the timing of decomposition signals in the simulated peat record, particularly those associated with changes in rainfall. The minima in fractional remaining mass associated with dry shifts occur in peat layers that are the same age as or older than the onset of the climatic excursion (i.e., the decomposition signal leads the climate driver) due to a falling water table re-exposing older peat, while wetting events cause increased preservation of peat formed at the time of the excursion and in the decades immediately after (a lagged signal; Figure 3g). Temperature-driven changes in net rainfall (via evapotranspiration) cause a similar temporal offset between climate driver and decomposition record (Figures 3f and 3h), although the offset is much less pronounced than in our independent rainfall manipulations (Figures 3e and 3g). In common with *Borgmark and Schoning* [2005] and *Payne and Blackford* [2008], we recommend that multiproxy reconstructions from peat records should account for the possibility that the timing of humification signals may be offset relative to other proxies for bog surface wetness from the same core (e.g., testate amoeba assemblages and plant macrofossils) and that the direction of this offset may vary depending on the direction of change in rainfall. Regardless of the direction of the change in rainfall, the magnitude of the temporal offset between climate driver and our simulated decomposition record increases with the magnitude of the change in rainfall (Figure 3g). The resultant chronological errors in humification records may be of the order of centuries or even millennia in the case of the largest climatic excursions.

Secondary decomposition causes a more severe loss of information from the final decomposition record for certain modes of climate change. Decomposition records of dry-wet-dry sequences, such as our representations of rainfall during the 4.2 and 2.7 ka B.P. events (Figure 4a), are particularly vulnerable to signal overwriting. The increase in peat preservation associated with the initial cooling, wetting phase of the excursion lags climate and therefore affects many of the same peat layers as the leading signal caused by the subsequent warming, drying phase: decomposition signals from the two phases of the excursion therefore partly overlap in the peat profile and are superimposed onto one another. The decomposition signal associated with a dry-wet-dry sequence is thus diminished (Figure 4d) compared to that caused by a lasting change in rainfall or temperature (e.g., dry-wet; Figures 2 and 3).

The published chronologies that we used to delimit our model representations of the 4.2 and 2.7 ka B.P. events are between 400 and 700 years in duration. Such events are slow enough that they avoid the low-pass filter proposed above, but may be obscured by the high-pass filter, allowing the simulated peatland to self-adjust and overwrite the climate signal if the magnitude of climatic change is not sufficiently large. Our smaller-magnitude representations of the 4.2 and 2.7 ka B.P. events (e.g., 100 mm yr^{-1} increase in rainfall with 1°C temperature decrease) are barely identifiable in simulated water-table depths and final decomposition profiles (Figures 4c and 4d). Our simulations illustrate how a number of ecohydrological mechanisms may combine to obscure climate signals in peat records and offer several potential mechanistic explanations for inconsistencies between reconstructions beyond genuine interregional climatic variability [cf. *Roland et al*., 2014].

4. Conclusions

Autogenic changes in peatlands and their potential to obscure climate signals have been discussed for at least 40 years, yet our work represents the first mechanistic attempt to understand and quantify them. Our simple—albeit plausible—simulations of bog development produced numerous complex behaviors, some of which are perhaps initially surprising, but all of which are easily explained through a consideration of the interactions between peat formation, decomposition, changes in pore structure, and hydrological processes. While our simulations support the notion of climate signal preservation in bogs in broad terms, they lead us to recommend the following:

1. Humification signals, unlike other peat climate proxies (e.g., plant macrofossil and testate amoeba assemblages), are likely to lag (wet shifts) or lead (dry shifts) changes in rainfall due to secondary decomposition;
2. The magnitudes of humification signals in response to dry-wet-dry sequences are likely to be subdued compared to other climatic sequences due to signal overwriting;
3. Peat records seem unlikely to provide reliable information about slow (e.g., millennial) changes in rainfall due to negative feedbacks between ecohydrological processes outpacing allogenic influences (a high-pass filter for climate information);

4. Short-term changes (e.g., annual to decadal) in rainfall and temperature are unlikely to be preserved in humification records due to secondary decomposition (low-pass filter), although the same problem is not apparent for other proxies. The combination of high- and low-pass filters means that large-magnitude climate events of intermediate time scales (multidecadal to centennial) may be most readily detectable in peat records;
5. Temperature changes appear to bypass some of the mechanisms which provide bogs with resistance and resilience to rainfall changes (namely, changes in hydraulic properties and drainage) and may therefore be better preserved in peat records.

Acknowledgments
All primary data generated by this study (i.e., model outputs) are freely available from the authors upon request by e-mail: p.j.morris@leeds.ac.uk or paul.john.morris@gmail.com. All model code is available in Software S1 and S2 in the supporting information. The gridded European multiproxy reconstructions used to represent Holocene climate are available from cited references [*Luterbacher et al.*, 2004; *Mauri et al.*, 2015; *Pauling et al.*, 2006; *Xoplaki et al.*, 2005]. Instrumental data for the Stonyhurst Observatory (see Text S1) are publicly available from climexp.knmi.nl/. Instrumental weather data for the Eskdalemuir (see Text S1) and Malham Tarn weather stations are available from the UK Met Office, subject to application: enquiries@metoffice.gov.uk. Dylan M. Young is supported by a NERC/ESRC interdisciplinary PhD studentship (ES/I903038/1). We are grateful to Basil Davis for his assistance in interpreting the European precipitation reconstructions by *Mauri et al.* [2015] and to the UK Met Office for providing long-term instrumental weather data.

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