ECOHYDROLOGY
Ecohydrol. **4**, 1–11 (2011)
DOI: 10.1002/eco.191

Ecohydrology Bearings—Invited Commentary

Conceptual frameworks in peatland ecohydrology: looking beyond the two-layered (acrotelm–catotelm) model[†]

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ABSTRACT

Northern peatlands are important shallow freshwater aquifers and globally significant terrestrial carbon stores. Peatlands are complex, ecohydrological systems, commonly conceptualized as consisting of two layers, the acrotelm (upper layer) and the catotelm (lower layer). This diplotelmic model, originally posited as a hypothesis, is yet to be tested in a comprehensive manner. Despite this, the diplotelmic model is highly prevalent in the peatland literature, suggesting a general acceptance of the concept. We examine the diplotelmic model with respect to what we believe are three important research criteria: complexity, generality and flexibility. The diplotelmic model assumes that all ecological, hydrological and biogeochemical processes and structures can be explained by a single discrete boundary—depth in relation to a drought water table. This assumption makes the diplotelmic scheme inherently inflexible, in turn hindering its representation of a range of ecohydrological phenomena. We explore various alternative conceptual approaches that might offer greater flexibility, including the representation of horizontal spatial heterogeneity and transfers. We propose that the concept of hot spots, prevalent in terrestrial biogeochemistry literature, might be extended to peatland ecohydrology, providing a more flexible conceptual framework. Hot spots are areas of a peatland which exhibit fast processing rates in a number of mechanistically linked hydrological, ecological and biogeochemical processes. The complementary concept of cold spots may also be useful in peatland ecohydrology, particularly with regards to understanding the vulnerability of peatlands to disturbance. The flexibility of our suggested scheme may allow the future incorporation of ecohydrological phenomena yet to be identified as important in peatlands. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS groundwater mound hypothesis; mire; diplotelmic model; conceptual model; hot spot; cold spot

Received 18 October 2010; Accepted 4 December 2010

INTRODUCTION

Background

Northern peatlands are important in their roles as shallow freshwater aquifers and globally significant terrestrial carbon stores (Gorham, 1991; Smith *et al.*, 2004). The long-term development of peatland ecosystems and soils is regulated by a network of interacting feedbacks between plant ecology, soil biogeochemistry and ground- and soil-water hydrology (Belyea, 2009; Eppinga *et al.*, 2009a,b). Such feedbacks between ecological and hydrological processes mean that peatlands may be thought of as prime examples of ecohydrological systems (*sensu* Zalewski, 2000). Some aspects of peatland ecohydrology not only exhibit complexity but also contain strong memory effects, leading Belyea and Baird (2006) to suggest that peatlands may be complex adaptive systems. Depth is a powerful predictor of a number of important ecohydrological variables in peatlands, including saturation, redox potential, soil structure and carbon quality. However, horizontal heterogeneity also appears to be important to transfers of water, nutrients and energy and to the shape of many depth relationships in peatlands (Bridgham *et al.*, 1996; Baird *et al.*, 2008; Eppinga *et al.*, 2009a). Despite this apparent complexity, it is common for discussions regarding peatland structure to default to the use of a simple one-dimensional conceptual framework, consisting of two ordinal layers: an upper, variably saturated 'acrotelm', a few decimetres thick, and a permanently saturated lower layer, the 'catotelm', commonly several metres thick (Ingram, 1978). This two-layered (or 'diplotelmic') model is probably now

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[†] A revised ecohydrology bearings paper for Ecohydrology.

at least 60 years old and the scheme's enduring popularity likely owes much to its simplicity, which would at first appear to confer general applicability. In this article, we explore whether the diplotelmic model is still valid in light of more recent research; we then suggest three possible alternative approaches and assess their usefulness in conceptualizing peatland ecohydrology.

Design criteria for a conceptual framework in peatland ecohydrology

Many natural science subjects have seen transitions over time between different conceptual approaches. Here we use the example of conceptual developments in catchment hydrology to illustrate the importance of three criteria against which we might measure a conceptual framework for peatland ecohydrology. Simple runoff generation concepts became popular in the mid-20th century (Betson, 1964; Hewlett and Hibbert, 1967), largely due to the simplicity and general applicability of those schemes. Their wide application provided a platform for increasingly reductionist field investigations of hydrological flow paths (e.g. transmissivity feedback, macropore flow) at a range of scales. These efforts led to a greater understanding of the complexity and uniqueness of watersheds (Beven, 2000; Tetzlaff *et al.*, 2008), exemplified by the concepts of runoff generation and contributing area variability as a continuum on the landscape (Beven, 2000). However, models that incorporate greater realism and complexity have often proved to be data-hungry and difficult to parameterize. Recent conceptual developments in catchment hydrology have therefore begun to move back towards a search for fundamental organizational principles and unifying ideas in order to generalize complex principles into simple rulesets (Beven, 2000; McDonnell *et al.*, 2003; Spence and Woo, 2003). The example of watershed hydrology serves to illustrate that, like all conceptual approaches, a conceptual framework for peatland ecohydrology should strive for a balance between explanatory power (i.e. a representation of real-world complexity) and simple, generalistic rulesets. A major goal of this paper is to evaluate the diplotelmic model in light of three criteria:

1. Complexity: The long-term development of peatland ecosystems and soils, as well as their short- to medium-term responses to disturbance, is governed by a complex web of interacting hydrological, ecological and biogeochemical feedbacks across a range of spatial and temporal scales (Vitt *et al.*, 2000; Belyea and Baird, 2006; Yu, 2006; Ise *et al.*, 2008; Belyea, 2009). Recent research indicates that horizontal spatial heterogeneity in peat properties, structures and process rates plays a key role in regulating various aspects of peatland system behaviour (Lapen *et al.*, 2005; Baird *et al.*, 2008; Eppinga *et al.*, 2009a). Models that neglect some of these feedbacks or the role of spatial heterogeneity risk misrepresenting system-scale behaviour (Belyea, 2009; Eppinga *et al.*, 2009a). Attempts to account for spatial variability by weighted averaging risk oversimplifying the effects of nonlinear relationships (Baird *et al.*, 2009). Therefore, the ability to account for spatio–temporal heterogeneity and complexity appears to be important requirements for a conceptual framework of peatland ecohydrology.
2. Generality: While accounting for complexity is important, it is also often highly desirable to be able to reduce complex processes and their interactions to simpler rulesets, so as to confer general applicability and to enable rule-based modelling of peatland behaviour (cf. Goldenfeld and Kadanoff, 1999). Furthermore, this generality should extend to a representation of multiple peatland types or forms. Raised bogs have arguably been over-represented in previous conceptual modelling schemes, at the expense of other peatland types such as fens, blanket bogs and permafrost collapse scars (Ingram, 1982; Clymo, 1984; Belyea and Baird, 2006; Swanson, 2007; also see Yu *et al.*, 2009). Balancing generality with an appropriate degree of complexity is a key challenge in the development of a conceptual framework for peatland ecohydrology.
3. Flexibility: Ecohydrological principles cannot always be rigidly and unilaterally defined, meaning that flexibility in the conceptual representation of peatland ecohydrology is desirable to account for the inherent variability in nature. Flexibility in conceptual models allows new theoretical developments to be incorporated and allows application to a wide variety of research questions. Conversely, conceptual models that are rigidly defined risk being viewed as obsolete, eventually to be replaced, in the light of new advances and may be of limited utility outside the specific use for which they were originally conceived. The impacts of disturbance on peatland ecohydrology provide a relevant example of the need for flexibility in conceptual models. Peat soils are globally significant stores of organic carbon (Gorham, 1991; Smith *et al.*, 2004) and there is concern that this carbon store may be vulnerable to disturbances such as wildfire (Turetsky *et al.*, 2004; Wieder *et al.*, 2009), drainage for agriculture and harvesting for fuel or horticulture (Van Seters and Price, 2001), permafrost degradation (Camill, 2005; Turetsky *et al.*, 2008) and climate change (Ise *et al.*, 2008). In many cases, disturbances can result in alterations to the peat profile through the loss of, or damage to, several centimetres or decimetres of peat. A conceptual framework that allows for, e.g. changes in the depth relationships of relevant peat properties, would therefore be of great utility in understanding the effects of various types of disturbance upon peatland ecohydrology.

THE DIPLOTELMIC (TWO-LAYERED) PEATLAND

History and terminology

The concept of the two-layered peatland appears to have originated in the Soviet literature during the mid-20th century and its first appearance in English-language literature is in Ingram's (1978) translation of Ivanov's (1953) work. In addition to first introducing the terms acrotelm,

DOI: 10.1002/eco

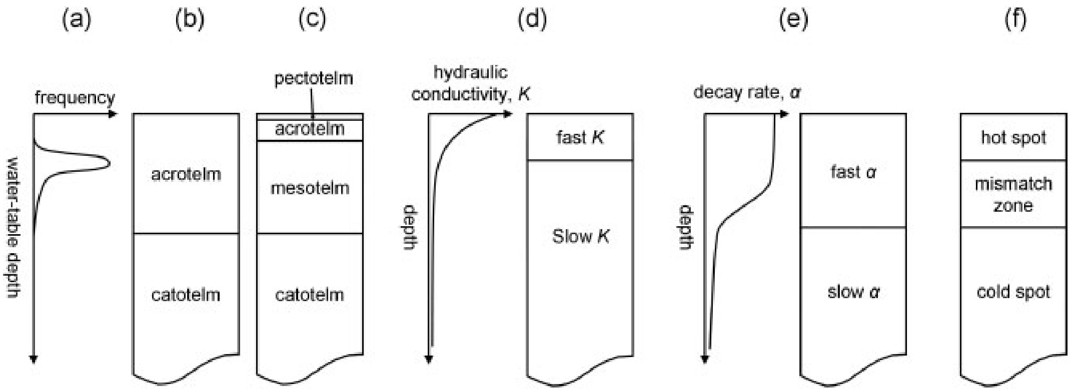

Figure 1. Hypothetical peat depth profiles showing (a) frequency distribution of water-table depth, (b) acrotelm and catotelm layers, according to Ingram's (1978) definition, (c) Clymo's suggested polytelmic model, including the mesotelm (defined by the range of all water-table positions) and the pectotelm, (d) continuous variations in hydraulic conductivity and classification onto dichotomous layers, (e) continuous variations in peat decay rates and classification onto dichotomous layers, (f) combination of (d) and (e) to show the location of the hot spot, cold spot and a zone of mismatch (refer main text for full description).

catotelm and diplotelmic, Ingram (1978) sought to improve upon Ivanov's earlier scheme by removing overlaps between the definitions of the upper and lower layers. Ingram (1978) stated that the true, unambiguous division between the acrotelm and catotelm should be the lowest position to which the water table falls during a drought year (Figure 1a and b). Ingram elaborated little in his 1978 work as to why this seemingly obscure hydrological metric should be of central importance to peatland ecohydrology, although the matter is clarified by a consideration of his later description of the highly influential groundwater mound hypothesis (GMH) (Ingram, 1982; see also Childs and Youngs, 1961). The GMH states that the maximum central height and overall shape to which a mature raised bog may grow are determined by the shape of the groundwater mound during drought conditions. The theoretical basis for the hypothesis was that any peat above the drought water table (i.e. the acrotelm, by Ingram's definition) is exposed, even if only infrequently, to oxic conditions and is therefore subject to high decay rates (Moore and Basiliko, 2006; Moore *et al.*, 2007), preventing the acrotelm from becoming more than a few decimetres thick. As such, Ingram devised the diplotelmic model on a truly ecohydrological basis because the scheme represents interactions between groundwater hydrology and peat decomposition, albeit in a somewhat black-box manner. Clymo (1984) presented a mass balance model to investigate the mechanistic limits of peat bog growth, utilizing a concept similar to Ingram's (1978) diplotelmic model. Clymo partitioned the modelled peat column into two layers based on general decomposition characteristics: an upper, primary oxic layer where decomposition is relatively quick and a lower, primary anoxic layer where decomposition is relatively slow (Clymo, 1984). At the time, the conventional ecological terms for these layers were 'active' and 'inactive', respectively, which Clymo (1984) deemed to be misleading because decomposition in the lower layer is not inactive but merely slower. Instead, Clymo adopted the terms 'acrotelm' and 'catotelm' to describe his model layers. However, in doing so the hydrological and ecological application of the diplotelmic model became intertwined and eventually perceived as linked. It is interesting that notions of an inherently two-layered ecosystem exist in other areas of ecohydrology, such as Walter's (1971) simple two-layer hypothesis for predicting ratios of woody to herbaceous plants on the basis of soil moisture in drylands.

Prevalence in the literature

We were interested in exploring how influential and widely adopted the diplotelmic concept has become in the time since Ingram's (1978) and Clymo's (1984) original articles. We queried the ISI Web of Knowledge database (Thomson Reuters, 2010) for all articles that appeared under a topic search criterion of 'peatland' (Figure 2a) and the proportion thereof that cite publications using the terms 'acrotelm', 'catotelm' or 'diplotelmic' in the article title or keywords (Figure 2b). Nearly a third of all peatland articles published in 2009 cite works for which one or more of the terms 'acrotelm', 'catotelm' or 'diplotelmic' represent central themes (Figure 2b). Moreover, popular peatland science textbooks at undergraduate (Charman, 2002), intermediate (Rydin and Jeglum, 2006) and advanced (Wieder and Vitt, 2006) levels each contain dozens of uses of diplotelmic terminology. This suggests that the use of the terms acrotelm, catotelm and diplotelmic is widespread within peatland science, which might be taken in turn to suggest a general acceptance of the concept. However, it also seems clear that some authors use the terms acrotelm and catotelm not only according to Ingram's (1978) strict hydrological definition, but also according to a looser definition referring simply to shallow and deep peat layers, respectively. We next consider the applicability of the diplotelmic concept based on both the strict and more relaxed uses of the terms.

Assessing the diplotelmic model

Ingram (1978) formalized the diplotelmic model as a testable hypothesis, although it appears that the concept is yet to be comprehensively evaluated in the manner in which he originally intended. Building on discussions by

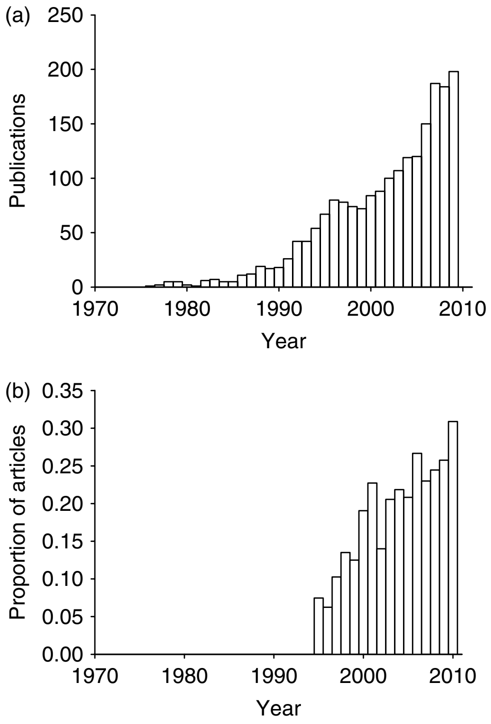

Figure 2. (a) Count of all published articles that appear under an ISI topic search criteria of 'peatland', (b) proportion of articles shown in (a) that also cite references that appear under a topic search criteria of 'acrotelm' and/or 'catotelm' and/or 'diplotelmic'.

Holden and Burt (2003), Belyea and Baird (2006) and Rydin and Jeglum (2006) and echoing Ingram's (1978) original intention for the concept, we ask: are peatlands well represented by discrete classification into the two ordinal layers acrotelm and catotelm? In order to address this question, we assess the diplotelmic model in light of the three criteria identified in Section 'design criteria for a conceptual framework in peatland ecohydrology'.

Complexity. The diplotelmic model meets our criteria for complexity in some respects, but not others. A two-way linkage is implied by the GMH (Ingram, 1982), based on the assumption that the lowest position of the water table controls peat decomposition, while decomposition (through its effect upon hydraulic conductivity—Rycroft *et al.*, 1975; Ivanov, 1981) in turn controls the water-table behaviour: a genuinely ecohydrological feedback. However, the diplotelmic model contains the implicit assumption that all ecological, hydrological and biogeochemical processes and structures can be explained in terms of a single discrete boundary—depth in relation to a drought water table. While depth is indeed a strong predictor of many variables relevant to peatland ecohydrology, the diplotelmic model's representation of depth and its reliance on a single threshold hinders its representation of a number of peatland ecohydrological phenomena, some examples of which we provide below.

For a hypothetical peatland, the frequency distribution of multi-year water-table position (Figure 1a) defines the boundary between the acrotelm and catotelm (Figure 1b) as the absolute lowest (drought) water-table elevation (Ingram, 1978). This hypothetical peatland could also be divided into discrete layers based on independent measurements of fast and slow hydraulic conductivity (Figure 1d) or peat decay rates (Figure 1e). In our example, the boundaries between the upper and lower layers are at different positions in the peat column, depending on whether one considers peat hydraulic conductivity or decay. While there is strong evidence of feedbacks between peat decomposition and soil hydraulic properties in peatlands (Rycroft *et al.*, 1975; Ivanov, 1981; Belyea and Baird, 2006), the relationship is complicated by multiple additional factors and any threshold changes in decay regime and hydraulic structure should not be assumed to be strictly coincident with one another. For example, peat hydraulic conductivity may be reduced by the presence of gas bubbles (mainly CH_4 as a biproduct of peat decay) (Beckwith and Baird, 2001; Baird and Waldron, 2003) and is also affected by changes in near-surface buoyancy that alter the surface elevation of the peatland, thereby shifting the positions of layers relative to one another. Moreover, changes in the elevation of the peatland surface in response to entrapped gas (Strack *et al.*, 2004) or water-table fluctuations (Price and Schlotzhauer, 1999) can cause decreases in hydraulic conductivity due to peat deformation (Whittington *et al.*, 2007), as well as changes in decay rates (Strack *et al.*, 2004). These kinds of interrelationships between important peatland hydrological and biogeochemical properties and processes cannot be represented within a rigid, two-layered scheme such as the diplotelmic model. A peatland surface that fluctuates in response to seasonal changes in water storage also partially undermines Ingram's (1982) assumption that static layers can be used as a predictor of the oxic zone thickness and water flux rates, thereby reducing the effectiveness of one of the scheme's main representations of complexity in peatland ecohydrology.

The diplotelmic model makes little allowance for horizontal spatial heterogeneity. Patterning of microforms such as hummocks, hollows and lawns appears to be an important manifestation of complexity, which arises from spatially variable transfers of water, nutrient and energy between microforms (Belyea and Baird, 2006; Eppinga *et al.*, 2009a,b). Furthermore, studies such as those by Mitchell *et al.* (2008) have indicated that the peripheral areas of raised bogs may exhibit qualitatively different biogeochemical regimes from the bog's interior, due to the chemical composition of runoff from surrounding mineral uplands. Thus, we argue that the diplotelmic model's inability to represent horizontal heterogeneity is an important limitation.

Peat pipes in blanket bogs are difficult to represent in a layered model without splitting the modelled peatlands into many high-resolution layers, with alternating high and low values of water flux rates (Holden and Burt, 2003), oxygen and dissolved organic carbon (DOC) content (Holden, 2005a) and decomposition (Holden, 2005b), in order to represent individual pipes or clusters of pipes. However, this scheme for blanket bogs would risk sacrificing generality for the sake of complexity.

It is apparent that the diplotelmic model in its current format is not capable of representing multiple aspects of ecohydrological complexity.

Generality. The diplotelmic model's greatest strength is arguably its simplicity; this simplicity affords the scheme general applicability. However, the application of Ingram's (1978) definition of the acrotelm *sensu strictissimo* appears to be operationally impossible, due to the ambiguity associated with the term 'drought-year water table'. Put another way, we might ask: what magnitude or return period of drought should be used to determine the acrotelm–catotelm boundary? Proxy evidence from peat cores suggests that, during severe droughts (e.g. return periods of the order of decades or centuries), peatland water tables may drop by more than 30 cm below their long-term average elevations (Booth *et al.*, 2006). By Ingram's (1978) definition then, the acrotelm–catotelm boundary should be well below what is usually (and observably) the hydrologically and biologically active layer and would incorporate much of what is commonly taken to be catotelm peat. A more practical scheme would be to define the boundary in terms of, for example, an annual (Ivanov, 1981; Wieder and Vitt, 2006) or five-year drought water table. The longer-term extreme low water table may be an important predictor of some aspects of peatland structure and function, most notably vegetation structure (Gignac, 2001), although it seems unlikely to be a stronger predictor of decay regimes than are seasonal and annual water-table regimes (Turetsky *et al.*, 2008).

It is easy to see that confusion could arise from inconsistencies in terminology depending on whether authors define acrotelm and catotelm according to Ingram's (1978) criteria, Clymo's (1984) decomposition-based interpretation, annual water-table fluctuations or other metrics such as threshold changes in bulk density or von Post score. This situation is easily remedied by authors taking care to clarify their definitions or by using alternative, more descriptive terms that are pertinent to the variables under consideration instead of acrotelm and catotelm (e.g. oxic/anoxic zones; saturated/unsaturated zones; mesic/humic—cf. Ise *et al.*, 2008; intact/collapsed layers—cf. Clymo, 1992). When interpreted in this more flexible manner, it is apparent that the notion of a peatland consisting of two distinct layers—not necessarily delineated by the drought-year water table—is a powerful concept that can explain meaningful variations in a number of response variables. For example, mean water-table position is important in controlling spatial variation in moss species composition (Gignac, 1992; Grosvernier *et al.*, 1997), while short-term fluctuations in the water-table position can serve as an important control on total decomposition rates (Moore and Dalva, 1993) and methane fluxes (Bubier *et al.*, 1993; Moore and Roulet, 1993; Bubier, 1995; Turetsky *et al.*, 2008).

Flexibility. The central tenet of the diplotelmic model is the coupling of processes and peat properties with depth, and specifically that changes in peatland processes are synchronous along the depth gradient (i.e. the state of all processes can be predicted based entirely on depth). We have already discussed how this assumption hinders a representation of a number of important ecohydrological feedbacks; these problems also relate closely to the flexibility of the scheme. While depth is indeed a powerful predictor of many variables of interest and while we may also see abrupt, threshold-like transitions in some variables with depth, it is difficult to justify beginning with the *a priori* assumption that all threshold changes occur at the same depth (drought water table) and can therefore be captured by a single, catch-all boundary.

The difficulties encountered in trying to represent peatland complexity within the diplotelmic model (refer Section 'complexity') would appear to arise directly from an inflexibility inherent in the model, because any and all threshold changes are assumed to occur at the same depth. For example, why should we expect any threshold change in decay rate to occur at the same depth as hydraulic conductivity (and indeed, at the same depth as threshold changes in all others variables)? This is an over-generalization that reduces the flexibility of the concept. We view this inflexibility in the diplotelmic model as an important limitation and one that is central to our discussion. Specifically, the lack of flexibility in the diplotelmic model limits its ability to represent the influence of disturbance (e.g. fire, drainage, harvesting, etc) on peatland physical and biological processes. Recent research has shown that disturbance can cause asynchronous shifts in physical and biological processes with depth (Waddington *et al.*, 2002; Turetsky *et al.*, 2007). In an undisturbed peatland, it might be reasonable to expect peat bulk density and saturation to co-vary with one another and to increase monotonically with depth. Disturbances such as peat consumption during wildfire or removal during peat harvesting can remove or damage the upper portion of the peat column, exposing previously buried peat and extending the oxic layer into older peat deposits (Price, 1997). Even if the saturation gradient returns to its predisturbance distribution, the bulk density gradient would have been irrevocably altered due to alterations in the structure of the peat column. Permafrost collapse can result in complete saturation of the peat column (Jorgenson *et al.*, 2006), thereby representing a 'haplotelmic' or single-layered peatland (Ingram, 1978) with anoxic conditions similar to that of the catotelm, while the bulk density and corresponding organic matter quality gradient remain unchanged, at least initially. Both examples illustrate that the asynchronous influence of disturbance on peat characteristics can have substantial influence on decomposition and peat accumulation regimes. The diplotelmic model's rigid definition of the acrotelm–catotelm boundary makes the representation within the model of asynchronous changes in peat physical and biological processes following disturbance challenging indeed.

A final pertinent question relating to the diplotelmic model's flexibility is how to represent 'fuzzy boundaries' in a two-layered scheme. In ecology, the identification of landscape-scale community transitions as either abrupt (ecotone) or gradual (ecocline) has received much attention in the last 20 years (van der Maarel, 1990; Attrill and Rundle, 2002; Dutoit *et al.*, 2007). We might apply a similar concept at a much smaller scale in order to describe within-peatland variations of ecohydrological properties and processes. Although threshold changes in space are conveniently represented by the definition of a boundary between discrete layers, some variables exhibit highly continuous variation that is not well captured by two layers. Beer and Blodau (2007) and Beer *et al.* (2008) showed that high porewater concentrations of dissolved inorganic carbon compounds, methane, phenols and other end products of peat decay can slow or even halt decay through thermodynamic limitation of microbial respiration (cf. Conrad, 1999). Beer and Blodau (2007) and Beer *et al.* (2008) postulated that deep layers in thick peat deposits may become effectively disconnected from rainfall due to slow porewater turnover times, allowing decay end products to accumulate in concentrations high enough to halt decay. This theorized deep zone of disconnection provides an example of a situation in which a two-layered scheme would struggle to represent the continuous down-profile variation of interest. In such situations it may seem tempting to discard the layer-based approach altogether and to give full consideration to continuous variation; however, such an approach risks sacrificing generality (also refer to Section on 'the continuum approach'). As a compromise, we might split the conceptual peatland into more than two layers. Specifically, the catotelm might be split into two layers, leaving three layers in total: a shallow, oxic layer where decay is rapid; mid-depths where conditions are anoxic and decay is slow, but non-negligible (not to be confused with Clymo and Bryant's (2008) proposed 'mesotelm', which consists of the deepest portion of Ingram's (1978) acrotelm—refer to Section on 'the polytelmic (many-layered) model') and a deep layer where porewater turnover is so slow that decay declines to negligible rates or even zero.

Assessment summary. The diplotelmic model offers a highly simplified framework for peatland ecohydrology; this simplicity affords the scheme general applicability, which would appear to explain much of its enduring popularity. However, as we have discussed, it is unable to account for a number of important facets of complexity in peatland ecohydrology, because it presents too rigid a scheme. These difficulties appear to arise from the lack of flexibility associated with the model's single boundary; we argue that it is therefore this inflexibility that is the root cause of the model's deficiencies. We recognize that in some cases it is convenient to split a peatland conceptually into discrete layers, sometimes even two layers. However, the *a priori* assumption that all variation in processes and properties of interest can necessarily be successfully represented by a single boundary—an assumption inherent in the diplotelmic model—seems difficult to justify. The diplotelmic model is also not well suited to peatland types other than raised bogs. It is arguable that due to advances over the last 25–30 years, peatland ecohydrology has in some ways outgrown the diplotelmic model.

BEYOND THE DIPLOTELMIC MODEL

We explore briefly three alternative approaches to conceptual modelling of peatland ecohydrology and assess their feasibility as frameworks for the subject. We make our assessment based on the three criteria identified in the Section 'design criteria for a conceptual framework in peatland ecohydrology'. However, having suggested that the diplotelmic model's main weaknesses arise largely from its inflexibility (refer Sections 'flexibility' and 'assesment summary'), we give particular attention to this criterion.

The polytelmic (many-layered) model

Clymo and Bryant (2008) discussed the need to expand the diplotelmic model formally by incorporating an additional layer, the 'mesotelm', between the acrotelm and catotelm. Clymo and Bryant (2008) proposed that the mesotelm represents the zone of seasonal variation in the water table, therefore consisting of the lowest portion of Ingram's (1978) acrotelm in which the water table fluctuates. Clymo also introduced the term 'pectotelm', representing the live photosynthetic plant layer at the very top of the peatland (R. S. Clymo, personal communication), resulting in a total of four structural layers (Figure 1c). Other conceptual layers might be required for particular research questions or peatland types, e.g. the frozen layer of peat in permafrost peatlands (i.e. the cryotelm).

It is easy to see how the scheme could be expanded further to include layers to represent a multitude of ecohydrological phenomena. Following our discussion on decomposition and water flux processes, we could include a deep layer of chemically inert porewater with long residence times (Beer and Blodau, 2007); multiple thin layers, in which water movements and decay are rapid, representing peat pipes in blanket bogs (Holden and Burt, 2003) and possibly tropical peatlands (Walsh and Howells, 1988); a near-surface layer of low permeability representing blockages in pore spaces by bubbles (Beckwith and Baird, 2001; Baird and Waldron, 2003). Ordinal layers could be developed for as many different processes as one's research questions dictated.

The polytelmic model potentially allows for the representation of greater complexity than does the diplotelmic model, but sacrifices some flexibility if layer boundaries are defined in universal terms. A polytelmic model in which layers are ordinally positioned with respect to one another still contains the implicit assumption that all peatland processes can be represented by a single, rigid scheme (depth). Such a model would lack flexibility in the same way that the diplotelmic model does by assuming that all peatlands can be represented by the same set of ordinal layers. The polytelmic model is also no better suited than the diplotelmic model to dealing with disturbance and spatial heterogeneity. Thus, we are unable to recommend the polytelmic model as a replacement for the diplotelmic model.

The continuum approach

Perhaps the most obvious approach to representing complexity in peatland ecohydrology (or indeed, in any

DOI: 10.1002/eco

subject) is an entirely reductionist one. Bridgham *et al.* (1996) discussed how peatlands may be represented by continuous hydrological, biogeochemical and ecological gradients. Some theoretical modelling studies (Hilbert *et al.*, 2000; Frolking *et al.*, 2001, 2010) have used simple mathematical rules to describe continuous changes in important one-dimensional (vertical) peatland state variables such as peat thickness and water-table depth. In the specific case of individual models, this kind of continuum approach potentially allows for a full representation of complexity in peatland ecohydrology (provided suitable rulesets can be identified—see Belyea and Baird, 2006) and is potentially highly flexible. However, a full continuum approach risks losing generality because it is difficult to envisage how it could be used as a framework for discussions on peatlands in general.

Hot spots and cold spots

Having identified that the diplotelmic model's inflexibility owes much to the assumption that all hydrological, ecological and biogeochemical processes are described by the same coupled layer boundary, we believe that the solution is simple: allow for multiple, asynchronous boundaries reflecting the processes and properties under consideration. Rather than using catch-all terminology such as acrotelm and catotelm, it may be more helpful for layers to be identified using more descriptive names such as oxic/anoxic zones (in reference to oxygen content), high decay/low decay zones (in reference to redox state) or mobile/immobile zones (in reference to water flux). Using simple, descriptive language such as this frees us from the rigid framework of the diplotelmic model and allows peatland scientists to be precise about their meaning. Under this more flexible scheme, it is possible to define as many layers and variables as required, thereby enabling the desired balance between complexity and generality for the question of interest without constraining the scheme by a single variable (drought water table).

Uncoupling of variables and their boundaries would facilitate the consideration of horizontal spatial heterogeneity, a key omission from the diplotelmic model. For example, Mitchell *et al.* (2008) found the edges of some peatlands to be important in regulating the production of methyl mercury due to the transport of solutes in upland runoff to the peatland perimeter. As an alternative example, we would still be able to identify a near-surface zone of high hydraulic conductivity (Ingram, 1978), but also a central zone of low mineral content (Mitchell *et al.*, 2008) or a marginal zone of low hydraulic conductivity (Lapen *et al.*, 2005; Baird *et al.*, 2008).

Clearly, our suggestion of using simple, descriptive terminology to describe dichotomous variation is not a new concept and it is evident that many peatland scientists already do this in their own work. However, our suggested flexible terminology allows the identification of separate zones of fast and slow processing in different variables and to consider the overlaps and mechanistic links among these zones. Of particular interest are those areas of peatlands where multiple rapid processes (e.g. water flux, decay rates, latent heat exchange) or high storage levels (e.g. oxygen availability, concentrations of DOC or growth-limiting nutrients) may be identified, particularly where mechanistic links cause the boundaries between layers to be broadly coincident. McClain *et al.* (2003) described areas within the landscape that exhibit disproportionately high rates of elemental cycling as biogeochemical 'hot spots' and suggested they are of key importance for resource management issues such as eutrophication, heavy metal transport and toxic algal blooms (another issue that is of relevance to dryland ecohydrology—Kingsford *et al.*, 1998). We suggest that the hot spot concept could be extended beyond its current use in describing some biogeochemical processes (e.g. McClain *et al.*, 2003; Mitchell *et al.*, 2008) and be applied to combinations of ecological and hydrological processes in peatlands. Following McClain *et al.* (2003), we define a hot spot as a three-dimensional zone within a peatland where ecological, hydrological and/or biogeochemical process rates are elevated relative to the rest of the peatland. These hot spots, which exhibit the most rapid transfers of mass and energy, are important for understanding system-scale behaviour. This is particularly true in areas where strong feedbacks may be identified between the processes of interest, because feedbacks between multiple processes appear to be highly important to determining the magnitude, and even the direction, of peatland response to perturbations (Belyea, 2009; Eppinga *et al.*, 2009b).

It could be argued that Ingram's (1978) and Clymo's (1984) acrotelm concept is an example of a hydrological and biogeochemical hot spot, in which partial aeration leads to rapid decay rates in near-surface layers. However, the diplotelmic model is only able to represent this one type of hot spot and only in one dimension. Other examples of hot spots that have been identified in peatlands include lagg fens, recognized as zones of high mineral and DOC concentrations and rapid exchanges of chemical energy and solute mass (Koprivnjak and Moore, 1992; Mitchell *et al.*, 2008), peat pipes in blanket bogs, which act as conduits for water, oxygen and DOC into and out of the peat profile, and are localized areas of rapid decomposition (Holden, 2005b), the live plant layer, where photosynthesis leads to high rates of evaporative water loss, latent heat exchange and carbon sequestration (Kim and Verma, 1996) and areas of groundwater upwelling in fens, which exhibit high porewater dissolved mineral content (Almendinger and Leete, 1998). Most importantly to our argument, hot spots may be delineated not only with respect to depth (as in Ingram's (1978) original scheme), but also horizontally to represent two-dimensional or three-dimensional heterogeneity in peatland ecohydrology (Mitchell *et al.*, 2008).

The concept of 'cold spots' as the complement to hot spots may be equally important in understanding peatland ecohydrology. We define a cold spot as a zone where the ecological, hydrological and biogeochemical process of interest operate at slow rates or where the feedbacks and interactions between processes are inhibited in some way. Recent research suggests that cold spots may be particularly important in determining redox conditions and peatland vulnerability to disturbances. For example, the deep zone of porewater disconnection proposed by Beer and Blodau (2007) may be thought of as both a hydrological and biogeochemical cold spot in deep peat layers, where slow porewater turnover leads to slow decay rates. Another example of a cold spot would be those areas in blanket peatlands not readily drained by pipes, such that porewater may become highly reduced and water flux is slow (immobile water). In terms of disturbance, *Sphagnum* hummocks have been identified as 'cold spots' in terms of vulnerability to combustion because high water retention (even during dry periods) of hummock forming *Sphagnum* inhibit combustion during wildfire (Benscoter and Wieder, 2003; Benscoter *et al.*, in press). This results in desiccated *Sphagnum* hummocks (aka *Sphagnum* sheep) often being the only aboveground fuels remaining in peatlands following severe burning (Shetler *et al.*, 2008).

Suggestions for a flexible future

The concept of hot spots and cold spots still facilitates the classification of a conceptual peatland into just two layers, in situations where this assumption is reasonable. As such, the scheme offers compatibility with previous research that has utilized the diplotelmic model. Indeed, while the acrotelm concept may be interpreted as an attempt to define a hot spot, it is apparent that Ingram's (1978) catotelm concept in turn fits our definition of a cold spot, in which constant anoxia leads to low decay rates, which Ingram (1982) later theorized to be the primary driver of the long-term accumulation of peat. However, our proposed scheme offers a greater flexibility than the diplotelmic and polytelmic models. The identification of hot spots and cold spots in any ecological, hydrological or biogeochemical terms allows for the definition of multiple discrete zones in a peat profile; the number of those zones, their horizontal configuration and perhaps most importantly their relative positions with depth, are not fixed. We do not suggest that a single, rigid scheme should be fitted to all peatlands. Rather, we suggest that the relative position and sizes of hot spots and cold spots are entirely flexible and should be tailored according to the study site and the research questions at hand.

This flexibility allows the representation of any number of processes and their interactions, providing a framework within which to discuss complexity (in terms of autogenic feedbacks) and the effects of disturbance (i.e. allogenic influences) across multiple peatland types, while using a single, consistent set of terminology. However, the flexibility in hot/cold spot terminology introduces the risk of ambiguity and confusion between studies. Authors should therefore take care to state clearly the terms in which they define their structural and functional zones in order to guard against ambiguity.

PRIORITIES FOR FUTURE RESEARCH

We suggest four areas of future research that would aid conceptual understanding of peatland ecohydrology.

1. Identifying mismatch zones: It may be possible to identify zones immediately around hot spots which exhibit fast processing rates in one respect (e.g., high peat decay rates) but slow rates in another (e.g. slow hydraulic conductivity). Given that the two processes combine in a mechanistically linked manner to produce a hot spot, areas where their boundaries are not entirely coincidental are interesting to consider (Figure 1f). In ecological research, increasing attention is being drawn to hypotheses concerning 'mismatches' in a variety of contexts, such as mismatches between phenotypes and the environment (Saino *et al.*, 2010) or mismatches between organisms and resources that they depend upon (Durant *et al.*, 2007). Here, we might consider ecohydrological mismatches, such as where the relationship between peat decay and hydraulic conductivity (Boelter, 1969; Rycroft *et al.*, 1975; Ivanov, 1981) breaks down. The identification of zones of mismatch between hydrological, ecological and biogeochemical processing rates would validate the need for our suggested decoupling of boundaries. The presence of zones of mismatch would support our assertion that the diplotelmic model lacks the necessary flexibility to provide a full representation of complexity in peatland ecohydrology. Identifying the existence of such zones in different peatland types or following various disturbances represent a logical next step in assessing whether the hot/cold spot model should be applied more generally to peatland ecohydrology, beyond its current applications in specific areas of biogeochemistry.
2. Combination of variables: Having demonstrated the need for variables in certain ecological, hydrological and biogeochemical processes to be decoupled from one another, we nonetheless recognize that being able to combine some processes into a common zone or gradient is desirable in order to aid generality. Beginning with the *a priori* assumption that all processes vary independently of one another would serve to overcomplicate and likely overparameterize models of peatland ecohydrology and is just as problematic for a conceptual model as the diplotelmic model's assumption that all variables co-vary with one another. Thus, an important area of research is to explore what approaches to vertical or horizontal zonation would produce the most parsimonious model of peatland ecohydrology. To achieve this, more information is needed on which variables exhibit consistent covariation and possess similar thresholds, allowing them to be grouped conceptually into a single hot or cold category or zone.
3. Identifying additional cold spots: Much recent and ongoing work examines the roles of ecohydrological hot spots in mediating peatland responses to both autogenic and

allogenic influences. We suggest that, by comparison, cold spots are comparatively poorly understood. The recent identification by Beer and Blodau (2007) of a deep zone of porewater disconnection, in which decay is thermodynamically inhibited, would appear to represent an important addition to conceptual models of peatland ecohydrology and is of relevance to peatland development and resistance/resilience to disturbance. The question of whether additional cold spots can be identified, particularly ones which confer resilience upon peatlands, is topical in the face of concerns that the peatland carbon stock may be a vulnerable one.

4. Role of disturbance: The role of disturbance in regulating the distribution of hot spots and cold spots may be important for understanding peatland function and vulnerability to changing disturbance regimes. Recent studies (e.g., Ise *et al.*, 2008) have suggested that positive feedbacks between changing climate and increased peat decay may override the negative feedbacks driving the self-dampening behaviour of peatlands (i.e. reduction of cold spots resulting in increased peat decay and release of carbon gas), causing a rapid loss of the peatland carbon stock, even from the deepest peat layers. Additionally, peatland disturbance due to land-use change both within peatlands (e.g. conversion to agriculture) or at their periphery (e.g. clear-cutting of adjacent upland forest or road construction) can alter not only the distribution of hot and cold spots but the relative importance of ecohydrological variables and processes. Future research should focus on the interactions between disturbances (e.g. fire, drought, peat harvesting, land-use change, climate change) and the distribution and relative sizes of hot/cold spots.

We believe that our suggested hot/cold spot scheme represents a more intuitive and flexible framework within which to discuss the ecohydrology of both pristine and disturbed peatlands than does the diplotelmic model, without sacrificing generality. In particular, flexible definitions of layer boundaries in any metric of interest may help to facilitate the future inclusion of processes and feedbacks that are yet to be identified as important.

ACKNOWLEDGEMENTS

We thank the editorial board of Ecohydrology, particularly the Associate Editor for Ecohydrology Bearings, David Breshears, for the invitation to contribute this piece. An anonymous reviewer provided helpful suggestions for improvements to an earlier version of the manuscript. Much of the inspiration for this piece arose from many interesting discussions with colleagues including (in alphabetical order) Andy Baird, Lisa Belyea, Jill Bubier, Christian Blodau, Jennifer Harden, Nick Kettridge, A. David McGuire, Tim Moore, Jonathan Price, Nigel Roulet, Maria Strack, Dale Vitt and R. Kelman Wieder. This research was partially supported by a NSERC Discovery Accelerator Supplement grant to JMW.

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