The changing water cycle: the Boreal Plains ecozone of Western Canada

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The Boreal Plains Ecozone (BPE) in Western Canada is expected to be an area of maximum ecological sensitivity in the 21st century. Successful climate adaptation and sustainable forest management require a better understanding of the interactions between hydrology, climate, and vegetation. This paper provides a perspective on the changing water cycle in the BPE from an interdisciplinary team of researchers, seeking to identify the critical knowledge gaps. Our review suggests the BPE will likely become drier and undergo more frequent disturbance and shifts in vegetation. The forest will contract to the north, though the southern boundary of the ecotone will remain in place. We expect detrimental impacts on carbon sequestration, water quality, wildlife, and water supplies. Ecosystem interactions are complex, and many processes are affected differently by warming and drying, thus the degree and direction of change is often uncertain. However, in the short term, at least, human activities are the dominant source of change and are unpredictable but likely decisive. Current climate, hydrological, and ecological monitoring in the BPE are limited and inadequate to understand and predict the complex responses of the BPE to human activities and climate change. This paper provides a case study of how hydrological processes critically determine ecosystem functioning, and how our ability to predict system response is limited by our ability to predict changing hydrology.© 2015 Wiley Periodicals, Inc.

INTRODUCTION

Changes in climate are giving rise to altered water cycles around the globe, raising issues of direct consequences for humans and the ecosystems we depend on. Canada is one of the world’s most water-rich nations; nevertheless, alterations to hydrological processes and water availability will have important societal and ecological impacts. In particular, changes to hydrological and ecological patterns and processes within the boreal forest may be significant at local to global scales.¹ Globally, boreal forests store a large proportion of the world’s terrestrial carbon (C) pool (23–31%) making the ecological dynamics of this system of considerable importance.² In Canada, boreal forests are home to about 3.7 million Canadians and major resource extraction industries. Sustainable management of water and water-dependent resources requires an understanding of how ecosystems are likely to respond to coupled changes in climate and the water cycle. Our goal is to assess the key sensitivities of hydrological processes and their interactions with ecosystems that will shape responses to climate change within an economically and biologically important part of western Canada’s boreal forest: the Boreal Plains Ecozone (BPE; Figure 1).
The BPE is expected to be highly sensitive to changes in climate predicted for the 21st century, because of the interactions between disturbance, biota, and hydrology. In this paper, we place a particular emphasis on the terrestrial ecosystems of the southern portions of the BPE, since these are the areas which are most vulnerable to changes, and are also where most human activities (agriculture, forest harvesting, and infrastructure) are focused. The transitional nature of the BPE, where many forest species reach their southern climate limits, makes it a model ecosystem to study the key ecological processes and relationships that will drive responses of hydrological processes to current and future climatic variability.

Successful climate adaptation and sustainable forest management require a better understanding of relationships among ecosystem health, human activities, and hydrologic processes. To identify these relationships we have structured this study around three questions:

1. What are the key characteristics of the BPE that affect the hydrological processes important for ecosystem functioning at local and regional scales? (see CHARACTERISTICS OF THE BPE section)

2. What are the most climate-sensitive parts of BPE ecosystems and what hydro-ecological feedbacks will affect transient and long-term responses to climate change? (see HYDRO-ECOLOGICAL RESPONSES TO CLIMATE CHANGE section)

3. What are the missing pieces in our knowledge of the BPE’s key characteristics, processes, and feedbacks needed to better anticipate changes of importance to society? (see RESEARCH PRIORITIES section)

CHARACTERISTICS OF THE BPE

The BPE in Canada (Figure 1) is distinguished from its surroundings by geology, climate, and dominant vegetation. Geological boundaries define the transition between the BPE and the Boreal Shield and the Taiga Shield to the north, and the Rocky Mountains...
(Montane Cordillera Ecozone) to the west. The northeastern boundary with the Taiga Plains Ecozone is climatic—the Taiga plains are colder with extensive continuous and discontinuous permafrost. The southern boundary of the BPE with the Prairie Ecozone is defined not by geology, but by the transition from continuous to partial forest cover (Figure 1), to agricultural land, and grassland further south. The BPE contains a number of major river systems, including most of the Peace, Athabasca, and North Saskatchewan River basins, and considerable portions of the Churchill, Red Deer (a tributary of the South Saskatchewan) and Mackenzie River basins.

Geology and Soils
The BPE is characterized by thick (up to 300 m), heterogeneous glacial deposits, which make up the surficial geology. Underlying bedrock layers are sedimentary strata predominantly comprising sandstone, shale, limestone, and dolomite, and that in turn overlie the crystalline Precambrian shield, which outcrops to the north of the BPE in the Boreal Shield Ecozone. Bedrock aquifers do not play a significant role in the processes discussed in this paper. Within the shallow glacial deposits, near-surface aquifers can be an important component of the hydrological cycle in the BPE, serving as a store and pathway for water and solutes. Mapping of surficial deposits in the BPE indicates that clay-rich glacial till and fine-grained glaciolacustrine deposits (hereafter “fine-grained deposits”) are the dominant feature of the surficial geology, with coarse-grained glaciofluvial and glaciolacustrine deposits (hereafter “coarse-grained deposits”) also important. These substrates function very differently and act as important controls on the hydrological processes (see Hydrological processes section and Synthesis: A conceptual model of the BPE hydro-ecology section).

Upland soils are strongly associated with parent material, with Luvisols, featuring a clay-rich B horizon, associated with fine-grained deposits, and Brunisols associated with coarse-grained deposits (Figure 2). Lowland areas that are wetter and hence anaerobic for much of the time feature Gleysols. About 21% of the BPE, mostly in the flat lowlands, is covered by peat, defined as an organic soil layer thicker than 0.40 m.

Climate
The BPE has extreme annual variations in temperature, with long severe winters, and mild to warm summers. Based on 1981–2010 climatic normals (Environment Canada National Climate Data Archive), the mean annual temperature varies from ~3–4 °C in the south to ~−2 °C in the north, with corresponding January means of −10 to −22 °C and July means of 15–20 °C. Both precipitation and evapotranspiration are highest in the summer. Summers are short, but the growing season is sufficiently long, warm, and moist to sustain tree growth, with annual growing degree-days above 5 °C varying from ~1500 °C day in the south to 1200 °C day in the north. Mean annual precipitation varies between 430 and 640 mm, with the highest values in the uplands of northern and western Alberta and the eastern BPE of central Manitoba, and the lowest values in the central BPE (Environment Canada Adjusted and Homogenized Canadian Climate Data). The fraction of precipitation that falls as snow increases from between 21 and 31% along the BPE’s southern edge to almost 40% in the north and northwest. Snow cover typically lasts 4 months in the south and 6 months in the north. Indices of dryness, such as the Climate Moisture Index, show increasing dryness to the south, due to longer growing seasons and higher evaporative demands. The BPE is Canada’s driest boreal forest ecozone, still snowmelt and rainfall are usually sufficient to minimize soil water stress during the growing season, except in the forest-grassland ecotone.

Climate reconstructions from the Holocene (ca. 11,000 BP to present) show significant variations in air temperature and moisture in west-central Canada. Compared with the recent past, the early Holocene was warmer, and the late Holocene after about 5000 BP was cooler, with increased soil moisture at the BPE’s southern margin.

Vegetation and Landcover
The BPE is a mosaic of forests, wetlands, lakes, and grasslands shaped by the interplay of geomorphology, climate, hydrology, disturbance history, and
ecological succession. Landcover in the BPE is principally evergreen needleleaf forest (23%), deciduous broadleaf forest (19%), mixedwood forest (5%), treed (11%) and untreed (10%) wetlands, grassland and cropland (16%), shrubland (5%), open water (10%), and rock (1%). Grasslands, croplands, and deciduous forests dominate in the forest-grassland ecotone (Figure 1). Wetlands occupy poorly drained flat areas and depressions.

**Uplands: Forests**

Upland vegetation distribution within the BPE is determined at regional scales by altitudinal and latitudinal gradients in climate and at finer scales by geomorphology, in particular parent material, hill-slope position, slope, and aspect. These factors in turn determine soil drainage class, moisture availability, and nutrient pools. In the central portions of the BPE where up to 60% of forest may occur on level terrain, variations in soil texture and parent material have a dominant influence on drainage and water balance, and thereby emerge as major factors determining vegetation patterns. Within the core BPE, upstate jack pine (*Pinus banksiana*) and midslope black spruce (*Picea mariana*) tend to dominate well- or moderately drained sites with coarse-grained deposits, whereas trembling aspen (*Populus tremuloides*) or mixtures of aspen-white spruce (*Picea glauca*) dominate upland terrain with fine-grained deposits and higher nutrient availability. Stands of white spruce, black spruce and eastern larch (*Larix laricina*) are interspersed with wetlands in poorly drained flat areas and depressions.

Superimposed on the hydrologically controlled patterns of vegetation distribution are the successional patterns caused by disturbances such as wildfire, insects (see Wildlife section), and forest harvest. Fire is an important disturbance agent within the BPE, with highly variable fire cycle ranging from 15 to >1000 years, depending on location, vegetation type, and amount of forest clearing. Forest harvesting creates small individual disturbances that alter the spatial forest mosaic of the BPE. Because forest disturbance alters canopy structure and leaf area, changes in disturbance frequency can indirectly affect landscape patterns of evapotranspiration.

At the BPE’s southern extent, conifer-dominated forests grade into aspen woodlands that become increasingly fragmented until grasslands dominate. The northern edge of the forest-grassland ecotone (Figure 1) coincides with a water-balance threshold in precipitation (P) minus potential evapotranspiration (*E*<sub>p</sub>), with wetter conditions in the forest-dominated portion of the BPE to the north, but *P* and *E*<sub>p</sub> still very closely balanced. During the earlier and warmer part of the Holocene, until about 5000 BP, the southern extent of the forest occurred several hundred kilometers north of its current position during the late Holocene. Prior to European settlement, climate controls interacted with the high flammability of grassland fuels to support frequent fires that constrained forest encroachment into grassland-dominant areas. More recently, fire suppression combined with agricultural encroachment into the forest have resulted in a complex spatial mosaic of forest, cropland, and grassland in the forest-grassland ecotone (Figure 1).

**Lowlands: Wetland and Lakes**

Water storage at or near the surface is a prominent feature of the BPE, particularly when compared to the grassland ecosystems to the south. Open-surface waters are abundant, from small ephemeral ponds to large lakes, with water quality ranging from eutrophic and hyper-eutrophic to clear oligotrophic or mesotrophic conditions. Groundwater inflows to these lakes are relatively small in the parts of the BPE where the surficial geology consists of fine-grained deposits, but lakes in coarse-grained deposits have strong groundwater interactions.

Peatlands are the spatially dominant wetland type throughout the BPE, except for the forest-grassland ecotone where non-peat-forming shallow marshes with emergent soft-stemmed aquatic plants are typical. Wetland type is strongly determined by the sources of inflow and thus is sensitive to climatically controlled shifts in the water balance. Peatlands, both bogs and fens, are permanently water saturated and are primarily fed by precipitation, but fens also have significant groundwater input that brings in additional nutrients. Marshes are fed by precipitation and surface runoff, but dry out periodically so that there is less accumulation of organic matter. Southward expansion of peatlands to their present limit coincided with the southward shift in the forest-grassland boundary about 5000 BP.

**Hydrological Processes**

**Evapotranspiration**

The diverse land-cover types in the BPE have markedly different rates of evapotranspiration (*E*), related to differences in leaf area index (LAI) and available soil water capacity. Evergreen needleleaf stands have lower summer LAI than broadleaf deciduous stands and hence transpire less (2–3 mm day<sup>−1</sup> for evergreen stands vs up to 5 mm day<sup>−1</sup> for deciduous stands). Although broadleaf stands transpire for shorter periods than conifers, their annual evapotranspiration is typically higher and more variable among years.
Evaporation from intercepted rainfall varies from 3% (open section of regenerating pine stand) to 37% (under mature spruce trees) of total summer $E$.\textsuperscript{27} Evaporation from lakes and ponds ($\sim$10% of area) is strictly limited to the open-water period and annual rates are comparable to or greater than precipitation ($P$).\textsuperscript{28} Effective precipitation (i.e., precipitation minus evaporation), therefore, is generally (but not always) positive, and highly variable spatially and temporally.

Long-term measurements of the stand-scale water balance for representative BPE landcovers at the Boreal Ecosystem Research and Monitoring Sites (BERMS) flux towers (Figure 1), previously reported by Zha et al.\textsuperscript{24} and Barr et al.,\textsuperscript{29} are updated in Figure 3. Of the three measured water-balance terms ($P$, $E$, and change in storage, $\Delta S$), $E$ has the lowest inter-annual variability but the highest variability among sites, ranging from 250 mm year$^{-1}$ for harvested jack pine to 433 mm year$^{-1}$ for aspen and 441 mm year$^{-1}$ for fen. The vegetation’s capacity to drawdown soil moisture at these sites during dry periods, as evidenced by the high inter-annual variability in $\Delta S$, buffers the inter-annual variability in $P$.\textsuperscript{24} The inferred stand-level lateral outflow $R$, estimated as $P - E - \Delta S$, has high variability among both years and vegetation types, with mean runoff ratios ($R/P$) of 10% (aspen), 11% (fen), 26% (black spruce), 29% (jack pine) and 38% (harvested jack pine), compared with 25% for gauged streamflow at the basin scale.

Evaporative losses from peatlands are subject to negative feedbacks associated with the water table depth, and sensitive to fire history, vegetation composition of the peat and the persistence of frozen layers after snowmelt.\textsuperscript{30} Over dry and wet years $E$ from an open fen, dominated by vascular plants, varied little and was about equal to the average evaporation from aspen forest, exceeding $E$ from mature black spruce and pine, as shown in Figure 3.\textsuperscript{29} Conversely, Gibson et al.\textsuperscript{31} found that catchments in the BPE with more wetlands had higher runoff ratios, implying lower evaporative losses from the peatlands than the forested uplands.

\textbf{Snowmelt and Runoff Processes}

Winter snow accumulation varies among vegetation types, depending primarily on canopy structure and LAI.\textsuperscript{32} Sublimation losses of intercepted snow range from 13% of annual snowfall in mixed stands of aspen and spruce, to 31% in jack pine and 40% in dense black spruce, while losses from open, burned and clear-cut areas are generally negligible.\textsuperscript{27} As a result, late winter snow cover is 30–45% less in coniferous forests than open areas and deciduous forests (which are leaf-free in the winter). Unlike open areas, forest sub-canopy snow cover is not significantly affected by wind redistribution.\textsuperscript{32} Forest canopies heavily attenuate the incoming shortwave radiation reaching the snowpack, especially given the low solar elevations in winter.\textsuperscript{33} Melt is up to three times faster in open areas, due to exposure to wind and radiation. However, longwave radiation emission from the canopy enhances net radiation at the snowpack and contributes significant energy for snowmelt.\textsuperscript{27}

Spring snowmelt leads to a peak in soil moisture levels, recharge to groundwater and wetlands, and lateral runoff, while the presence of frozen soils and organic soils strongly influences streamflow response.\textsuperscript{27,34} Most BPE soils are frozen at the time of snowmelt, which strongly influences lateral runoff. Soil freezing depths are greatest for thin snow covers, thin organic soil horizons, and low soil water contents. At the BERMS sites from 1999 to 2008 freezing depth varied from 0.4 to 0.8 m beneath black spruce, 0.0 to 1.0 m in a fen, 0.2 to >1.0 m beneath aspen, and consistently greater than 1.0 beneath jack pine. The infiltration capacity of frozen soils is severely reduced when the pre-freeze soil moisture content is high\textsuperscript{17,35} or when melt water refreezes creating “concrete frost” layers.\textsuperscript{34} Soils with macropores (i.e., most undisturbed soils) are more likely to have unrestricted infiltration capacities.\textsuperscript{35} As a result, the partitioning of melt between runoff and infiltration in the BPE is a dynamic and complex process, with controls that include soil texture and structure, pre-freeze water content, snow depth and timing of snow cover, rate of snowmelt, and energy available for melt (dependent on aspect, canopy cover, and weather conditions). For example, Redding and

![Figure 3](image_url) Inter-annual variability in the vertical water balance at the BERMS study sites in central Saskatchewan, for October to September hydrologic years between 1999 and 2011. $P$ represents precipitation, $E$ represents evapotranspiration (with an objective energy-closure adjustment of +18%), $\Delta S$ represents soil-water storage change, and $R$ is the inferred lateral outflow, calculated as $P - E - \Delta S$. The x-axis labels are vegetation type: A = aspen, S = black spruce, P = jack pine, H = harvested (juvenile jack pine), F = fen, and B = basin (gauged streamflow). The box plots indicate the 10th, 25th, 50th, 75th and 90th percentiles.
Devito\textsuperscript{34} carried out plot scale experiments in the Utikuma Region Study Area (URSA in Figure 1) and found that runoff generation was more strongly influenced by aspect than soil moisture content or soil texture. This was due to south facing slopes received more radiation, leading to more rapid snowmelt and periodic mid-winter snowmelt/refreezing events which caused the development of impermeable frost layers.

The surface runoff mechanisms discussed above and the subsurface flow mechanisms discussed in the next section result in active exchange of water between peatlands and surrounding hillslopes. The hydraulic properties of peat promote water retention when the water table is low, and water transmission when the water table is high.\textsuperscript{30,36} As a result peatlands can serve as water reservoirs, providing water to the surrounding landscape during droughts and absorbing extra water during wet years.\textsuperscript{29} In winter a solid frozen zone usually develops in the peat and can persist well into summer, so that after snowmelt open water can pond above the frozen zone, allowing rapid surface runoff.

**Subsurface Flow Regimes**

The subsurface flow regime in the BPE is controlled primarily by parent material. Fine-grained deposits have low permeability, but in the near-surface weathered zone there is considerable permeability and active storage capacity associated with the fractures.\textsuperscript{7} Lateral saturated flow is only significant when the water table is within a few meters of the ground surface (i.e., the transmissivity feedback mechanism), or when preferential flowpaths above frozen ground become activated (e.g., see Waddington et al.\textsuperscript{30}). In this setting, the water tables are generally shallow, hence evapotranspiration is not typically water limited (e.g., the BERMS black spruce site\textsuperscript{24}). In some settings, the water table below the upland may be deeper, due to the presence of an underlying regional aquifer, draining the shallow water table.\textsuperscript{37} The subsurface flow regime in fine-grained materials, and interactions with wetlands, are described in van der Kamp and Hayashi,\textsuperscript{7} and Smith and Redding.\textsuperscript{37}

In contrast to the fine-grained parent materials, landforms with coarse-grained deposits are highly permeable, with significant vertical drainage and groundwater recharge, deeper groundwater tables, and less water in the soil available to vegetation due to low water-holding capacity of the material.\textsuperscript{22} Lateral groundwater flow is significant and sustains baseflow throughout the year, which generally drains to fen complexes that border upland forests. Throughout the winter, groundwater drainage to fens can lead to artesian conditions below peatland ice cover.\textsuperscript{38}

### Synthesis: A Conceptual Model of the BPE Hydro-ecology

The hydrological regime of the BPE, and in particular runoff generation, is subject to the highly complex processes described above. The spatial configuration of controls (geology, soil, slope, aspect, and vegetation cover) makes generalizations about behavior a challenge, especially when combined with vast spatial scales and the scarcity of detailed observations. However, certain patterns across the landscape are understood to be broadly representative of the dominant system characteristics. Figure 4 presents a conceptual model for the dominant observed configurations of geology, soils, and vegetation cover, and the associated hydrological functioning. This model is particularly influenced by the hydrological conceptual models of van der Kamp and Hayashi,\textsuperscript{7} Smith and Redding,\textsuperscript{37} Devito et al.,\textsuperscript{17} and the landscape-vegetation model of Bridge and Johnson.\textsuperscript{15}

### HYDRO-ECOLOGICAL RESPONSES TO CLIMATE CHANGE

The BPE system is characterized by complex interactions and feedbacks between multiple processes and drivers of change. Figure 5 depicts the authors’ assessment of the dominant interactions that will dictate how the BPE is affected by climate change. Specific hypotheses on future responses are provided in RESEARCH PRIORITIES section.

#### Climate Change

Northern biomes, including the circumpolar boreal forest, are undergoing more rapid warming than other terrestrial biomes, driven primarily by a lengthening of the snow-free period and the associated albedo decline.\textsuperscript{39} The warming trend observed for much of Canada during the 20th century has been particularly strong in the western continental region, with a mean increase of 2.0°C from 1950 to 2003.\textsuperscript{40} Within the BPE, the reference climate stations (1950–2010) show greater warming in winter (2–3°C) and spring (1–2°C), relative to summer (<1°C or insignificant) and fall (insignificant), with slightly higher temperature increases at night than during the day.\textsuperscript{41,42} Although the winter warming trend has recently weakened or reversed sign over the Eurasian boreal forest (1998–2010), the positive trend has persisted for boreal forests in Canada and Alaska.\textsuperscript{43} The positive spring temperature trend at northern latitudes is associated with an advance in the timing of snowmelt.\textsuperscript{44}

In contrast to temperature, the observed precipitation trends are weaker and less certain; none of the reference climate stations within the BPE show
**FIGURE 4** | A conceptual diagram of the hydrological regime in the BPE.

**FIGURE 5** | The dominant controls of hydrological and ecological change in the BPE.
a significant trend in annual total precipitation over 1950–2010,42,43 although some show a significant decline in annual snowfall and the fraction of precipitation that falls as snow, associated with the shortening cold season.45 Paleolimnological studies show a drying trend in the northern BPE since 1850, coupled with reduced flood frequency.46

Future climate projections, based on an ensemble of models, show consistent warming at northern latitudes, with subtle differences in magnitude and seasonality.39 For the BPE, the ensemble of models used in the IPCC 5th Assessment Report forecast warming between 1.75 and 6°C over the 21st century, dependent on the emissions scenario. The projection is less consistent for precipitation and soil moisture change.39 Many global models show the Earth’s wet areas becoming wetter, and its dry areas becoming drier; however, the models diverge at regional scales47 and often the reported trends are not robust.48 In Canada’s western interior, the predicted temperature-driven increases in $E$ typically exceed the smaller increases in $P$, thus increasing the duration and intensity of moisture deficits. The predicted future drying trend is strongest in the prairie region south of the BPE, but a drying trend is also predicted for the southern BPE,40 albeit with a high level of uncertainty.47,49

Changes to BPE vegetation will cause feedbacks to the climate system, but at present the net warming/cooling effect is unclear because of multiple offsetting processes,51 including changes in the surface energy balance and greenhouse gas exchange. An increase in the fraction of open land, resulting from more frequent disturbance events and the northward movement of the forest-grassland ecotone, will have a net cooling effect caused by increased albedo, but damped by an increase in the Bowen ratio (i.e., an increase in sensible heat causing warming relative to latent heat consumed by evaporation).52 The net response of the BPE’s greenhouse-gas budget to global change is uncertain. Warmer springs and longer growing seasons will likely strengthen the forest C sink,53 but this effect may be overwhelmed by more frequent disturbance throughout the BPE and the change of forest to grassland in the southern BPE, both of which will reduce ecosystem C storage. The feedbacks to precipitation processes are even more complex and unclear, as evidenced in the high uncertainty in future precipitation projections (above).

Hydrologic Response
The boreal forest’s water balance is highly sensitive to climatic variability. The effect of the 2001–2003 drought4 on annual $E$ was much greater for the deciduous-broadleaf aspen site than that for the evergreen-needleleaf spruce and pine sites within the BERMS sites, but much greater still for a grassland in southern Alberta.24,25 A fen acted as a water source to the surrounding upland during a severe drought and a strong water sink following the drought.53 Streamflow was also highly variable, with streams in the fine-grained deposit areas drying out entirely by the end of 2003, while base flow persisted in the coarse-grained deposit areas due to groundwater discharge. The water levels of many lakes also declined below the outflow elevation so that the lakes became hydrologically isolated with no streamflow leaving the lakes. The implications for aquatic ecology and biogeochemistry of the lakes are not well understood.

The direct impact of climate change on hydrology is through changing precipitation and/or evapotranspiration (see Climate Change section). It is likely that this would result in drying (e.g., Stadt and Qualtriere43), but it is also likely in the long term that the upland vegetation would shift in response to drying (see Vegetation response section). Therefore, it is unclear what the impact would be on groundwater and surface water bodies (we provide hypotheses in RESEARCH PRIORITIES section).

In general, responses of hydrological processes to winter warming are highly uncertain. Earlier spring snowmelt and delayed autumn snowfall are predicted to be very likely,56 but due to the complex runoff generation mechanisms described in Snowmelt and runoff processes section, the impact of this is not clear. For example, earlier melt could mean a shift to an earlier peak in streamflow and less water available in the late summer.56 However, it could also mean more infiltration due to both a greater proportion of rainfall versus snowmelt and more snowmelt infiltration, which could increase stream baseflow and soil moisture. In RESEARCH PRIORITIES section we outline a number of specific hypotheses about how the BPE might respond to warming.

Vegetation Response
The BPE’s vegetation dynamics will respond to climate change in two ways: directly, via altered moisture and temperature stresses; and indirectly, via changes in the disturbance regime.

Direct Climate Change Effects
Changes in climate and water balance will have short- and long-term effects on the productivity, structure, composition, and distribution of boreal forest ecosystems.3 In the short term and in the absence of water stress, we expect increases in forest productivity associated with warmer temperatures,
rising atmospheric CO₂ concentration, and atmospheric nitrogen deposition. Observations from the BERMS flux towers show the dominant, positive influence of spring warming on net ecosystem production in both deciduous-broadleaf and evergreen-needleleaf forests.

In the long term, changes in the water balance are expected to have a major influence on BPE vegetation, although the processes are complex and poorly understood. Compared to other terrestrial biomes, the boreal forest is among the most likely to be affected by climate change. Climate change impacts on forest productivity and tree growth are already being documented across the boreal forests of North America and Eurasia, and are generally interpreted as signals of increasing drought stress. Recent analysis of forest inventory data coupled with modeling show a widespread decline in tree growth and increase in stand-level tree mortality in the Canadian boreal forest, with a concomitant weakening of the boreal biomass C sink. The dominant contributor appears to be drought-induced tree water stress. Indeed, the southern boreal forest is likely an area of maximum ecological sensitivity in the 21st century due to the expected increase in moisture stress.

To date, the most significant structural changes have been observed in trembling aspen ecosystems in the drought-prone forest-grassland ecotone. These aspen-dominated woodlands, together with islands of forest dominated by jack pine, are likely to retract their range northwards in response to increasing moisture deficits (diminishing \( P - E_p \)). The recent 2001–2003 drought in western Canada caused severe dieback and mortality of aspen stands along the boreal-parkland ecotone. The importance of drought in controlling forest distribution and composition is also emphasized by the high correlation of dead trembling aspen biomass with drought severity in the southern boreal region. Consistent with these observations, dynamic vegetation models linked to climate output from general circulation models predict a contraction of the BPE at its southern limits due to moisture stress. However, these projections are uncertain, because climate models differ over the direction of regional precipitation trends, and also do not account for disturbance or changes in land use.

Not only do we expect a northward shift of the BPE’s southern limit in response to climate change, we also anticipate significant changes in the vegetation distribution within the BPE. Tree ring studies from across the circumboreal biome suggest that ecosystem vulnerability will vary by plant species and landscape position, because of the large differences in moisture requirements among species. Areas with strong edaphic controls on water drainage and moisture availability, such as lowland fens, may be buffered against the rapid changes in hydrology that would lead to dramatic shifts in vegetation type. However, most BPE tree species occupy discrete biophysical niches with well-defined bounds of soil-moisture availability, so that any changes in \( P \) or \( E \) that alter soil-water content will likely impact the distribution of land-cover types across the BPE landscape. We anticipate that a reduction in \( P - E_p \) will cause a shift in forest distribution along hillslope gradients, with expanding coverage of drought-tolerant vegetation such as jack pine woodlands that are currently characteristic of coarse soils and well-drained ridgetops. At the same time, we expect a contraction in the distribution of more drought-intolerant species, such as black spruce and their associated moss and sedge communities. The degree to which these shifts occur will depend heavily on the extent to which changes in hydrology are mediated by edaphic factors, such as moisture retention in fine-textured soils or poorly drained valleys and location within the local and regional groundwater flow system.

We have yet to see evidence of altered vegetation composition in undisturbed forests that can be reliably linked to hydrologic or other climate changes, either within the core BPE or in other boreal regions of Canada. There is substantial inertia associated with the persistence of existing vegetation cover caused by stabilizing interactions between environmental conditions and intact vegetation. This inertia may strongly influence both the timescale and pattern of vegetation responses to changing climatic and hydrologic conditions. As a consequence, vegetation responses to hydrologic change will likely be characterized by substantial time lags with discrete periods of rapid changes that are coupled with disturbance.

**Changes in the Disturbance Regime**

The greatest impacts of climate change on BPE vegetation dynamics may actually occur through indirect, disturbance-mediated processes. Studies of forest responses to disturbance within the greater boreal region suggest that fire, logging, or other landscape-scale disturbances may be interacting with climate change to alter the recovery patterns of boreal forests, and cause shifts in forest states. There is clearly a need to better understand the relative impacts of a direct forcing of changing moisture regimes on forest growth and mortality as opposed to moisture- and climate-mediated changes in the disturbance regime and forest resilience to disturbance. This issue is of particular importance within the BPE, where vegetation patterns are heavily influenced by widespread fire and human disturbance.
Disturbance effects on vegetation will be further mediated by impacts of climate change on the frequency, size, and severity of natural disturbances. Fuel moisture content, which is tightly coupled to the forest water balance, is the primary determinant of fire behavior in the boreal forest. Reconstructions of historic wildfires have shown that the annual area burned expands dramatically during prolonged and severe periods of drought. Fire dynamics modeling suggests that the BPE’s wildfire regime has recently shifted from subcritical to critical, and that wildfire may further intensify over time. Among circumpolar boreal forests, western Canada’s boreal forests appear to be particularly vulnerable to increasing wildfire regimes in the future, driven by the long-term drying of the forest floor. Insect outbreaks are also predicted to be more frequent and intense (see Wildlife section) as a result of climate change.

Disturbance events thus constitute the primary nexus for vegetation shifts to occur within the BPE. Unlike established forests and wetlands, which are relatively stable, young re-establishing ecosystems are dynamic and able to re-assemble along various species trajectories. Disturbances have the capacity to alter the forest’s response to changing environmental conditions in two ways: they interrupt the plant–environment interactions that stabilize vegetation communities within a given state, and they directly affect the subsequent direction of vegetation change through impacts on patterns of community re-assembly. However, the combination of community inertia and the sensitivity of community change to disturbance make it very difficult, perhaps impossible, to accurately predict the timing and pattern of vegetation shifts within the BPE in response to changing environmental conditions. Furthermore, the relationship between climate change and vegetation dynamics is difficult to interpret; patterns through time confound the two independent drivers of vegetation change—those driven by stress-induced mortality with those driven by successional processes. Consequently, monitoring of early warning signals and developing probabilistic estimates of landscape vegetation change are likely to be our best guides for anticipating future changes in forest vegetation in response to changing hydrologic regimes.

Wildlife

**Impacts of Wildlife on Hydrology**

Wildlife such as beaver (*Castor canadensis*), ungulates (moose, elk, whitetail deer, mule deer, and bison), and defoliating and tree-boring insects may drive changes in BPE hydrology. Beaver dams have various impacts on surface and subsurface hydrological processes and drive cascading effects on watershed hydro-ecology. Specifically, beaver dams: increase numbers of wetlands; increase evapotranspiration losses owing to greater open water extent and earlier ice-off; reduce downstream flows and attenuate seasonal flow fluctuations; and raise groundwater levels and enhance stream-groundwater interactions. Beavers also excavate canals on the margins of beaver ponds, which may increase surface water connectivity and initiate wetland drying.

Large ungulates affect hydrology directly by compacting soil and eroding pond and stream banks. Ungulates also consume and trample riparian vegetation, indirectly impacting surface hydrological processes and nutrient cycling. In some areas, the impact of ungulates on hydrology may exceed that of beaver.

Insect pests, including spruce budworm, jack pine budworm, and forest tent caterpillars, cause large-scale defoliation. Outbreak events cause widespread tree mortality that lowers forest transpiration, increases snow accumulation, and slows ablation rate. Researchers predict outbreak events to elevate understory evapotranspiration, and ground evaporation, though mountain pine beetle infestation did not affect evapotranspiration rates in lodgepole pine forest in British Columbia. Climate change is predicted to increase outbreak frequency and intensity, as outbreaks are associated with high temperatures and droughts, and insects cause greater damage to trees experiencing water stress.

**Wildlife Responses to Hydrological Change**

Hydrological change is expected to affect diverse wildlife groups both directly and indirectly via changes to plant communities. Drier conditions will most impact wildlife reliant upon water, including waterfowl and amphibians. Indirectly, vegetative responses to hydrological change may trigger trophic changes that cascade throughout the animal community. Drier conditions reduce the quantity and quality of forage for herbivores, and availability of suitable habitat for both birds and mammals. Conversely, large mammals may benefit from increased food availability in winter and reduced wolf predation as a consequence of reduced snow pack. Earlier snowmelt will spur earlier vegetation growth, resulting in a phenological mismatch for organisms like moose and long-distance migrant birds that reproduce at the same time each year. Birds may also experience elevated nest predation rates, as water stress may increase conifer cone production over the short term, benefiting nest-predating rodents such as red...
squirrels.90,91 This is of great concern, as a 50–70% decline in long-distance migratory birds—which protect boreal trees by keeping insect pests in check—is predicted to result in major changes to boreal forest tree species composition and, ultimately, hydrology.92

Biogeochemical Cycles
Biogeochemical cycles, which move chemicals from the environment into living material and vice versa, are critical to the hydro-ecological functioning of the BPE. These cycles depend most on temperature, which governs the rate of many processes, and water availability, which acts as a transport medium into/out of living material and between landscape components. Oxygen conditions are also strongly influenced by hydrology, and determine whether a system is a nutrient sink or source. These cycles determine productivity of terrestrial and aquatic systems, the water quality of surface waters, and the storage and release of greenhouse gases, all of which are sensitive to short- (seasonal) and long-term changes in climate and hydrology. Identifying potential impacts of climate-induced hydrological change on biogeochemical processes in the BPE is challenging. More research is needed considering linkages between climate and hydrology, biogeochemistry, and aquatic ecology in the region.

Nitrogen (N) is a limiting nutrient in BPE uplands,93 meaning any change in the N cycle will directly affect tree growth. As temperature and water availability change, key components of the N cycle (such as mineralization) are affected, but it is unclear whether or not warming-induced increases in productivity will exceed drying-induced limitations. In situations where N availability is increased and biomass removals through forest harvesting take place, other nutrients can become limiting, thus changing ecosystem dynamics.

Carbon (C) stored in boreal ecosystems may be vulnerable to a warming climate.94 Carbon dioxide (CO2) and methane (CH4) exchange between peatlands, surface waters, and the atmosphere are an important climate feedback. As noted above, the position of the southern extent of peatlands changed during the Holocene. Water table drawdown in peatlands may reduce gross primary production, enhance aerobic soil respiration, reduce methane emissions,95 and increase dissolved organic carbon concentrations.96

Drying of smaller open-water marshes and ponds (an important feature of the southern BPE) could lead to great hydrologic isolation, resulting in a reduction in nutrient and mineral influxes, though with potential to increase salinity and cycling of nutrients within standing water (i.e., internal loading).7

In boreal lakes, increased temperatures and resultant stratification can reduce the frequency of mixing of the water column, which can induce low oxygen conditions in the bottom waters, promoting internal loading of nutrients and the release of hydrogen sulfide and greenhouse gases from sediments. A reduction in the duration and frequency of ice cover associated with winter warming97 will have important implications for biogeochemical cycling in lake systems, owing to light availability and the potential for changes in the thermal mixing regime. Climate-assisted lake eutrophication has been documented at the northern extent of the BPE, attributed to nutrient release from sediments.98 Likewise, both Kurek et al.99 and Hazewinkel et al.100 identified recent (20th century) warming as the principle driver of increased lake productivity, leading to enhanced anoxia and changes in sediment redox conditions.

RESEARCH PRIORITIES
Our review of eco-hydrology in the BPE has led to the identification of critical knowledge gaps that we summarize in Boxes 1–6, with associated hypotheses.

BOX 1

A DRYING FOREST

What we know: Within the BPE, the dominant control on hydrological and ecological processes is \( P - E \) (precipitation minus evapotranspiration). \( P \) is relatively low and only slightly larger than \( E \), but the precipitation excess \( P - E \) is highly variable across years and among vegetation types, and hence water availability is extremely vulnerable to change.

Knowledge gap: We do not know how \( P \) will change under climate change. We expect \( E \) to increase under a warmer climate, but we do not know how this will be influenced by land-surface feedbacks, in particular associated with changing vegetation.

Hypotheses: Climate change-driven increases in temperature will drive increases in \( E \), which will exceed possible increases in \( P \), and hence \( P - E \) will tend to decrease on average. Less water will be released from the uplands and there will be enhanced evaporation from lakes due to higher temperatures, and longer ice off conditions. Falling water levels and reduced hydrological connectivity across the landscape will have detrimental impacts on water quality, wildlife, and water supplies.
A SHRINKING FOREST

What we know: The forest-grassland ecotone and the adjacent forests in the southern BPE are the BPE’s most vulnerable areas to climate change. They are located on a climatic tipping point along a north–south gradient in $P - E_p$, which decreases toward the south. This region is also subject to significant anthropogenic disturbances, notably forest harvesting and agriculture. In recent wet years, flooding has led to tree dieback and mortality in some locations. Countering these effects, the suppression of fire and reduction in herbivory since the onset of agriculture has led to a wide-spread increase of tree cover in part of the forest-grassland ecotone, especially in noncultivated areas.

Knowledge gap: Will increased water stress reverse the trend to increased tree cover in the forest-grassland ecotone that started with the elimination of natural disturbance? Or will human activities continue to exert the dominant control? What will be the rate and extent of deforestation in the southern BPE and how will this perturb land-atmospheric feedbacks and alter the regional climate?

Hypotheses: A reduction in plant water availability will cause some tree mortality directly, but the main impact on forests will be seen in an increase in natural disturbance events (fire, insects), and changes in the composition of species that regenerate post-disturbance via changes in species recruitment and re-establishment.

CHANGING FOREST COMPOSITION

What we know: The spatial distribution of BPE forest vegetation (tree and understory species) is strongly determined by moisture availability, which in turn is determined by soils/surficial geology, with two dominant functional soil/geology classes forming the BPE; however, forests are also subject to natural (fire, insects) and anthropogenic (harvesting, mining) disturbances, and regeneration post-disturbance could potentially result in shifts in species composition under a changing climate.

Knowledge gap: How will vegetation cover change in response to warming, in particular, post disturbance? Will some plant functional types or landscape positions be more resilient than others, for example a shift toward more grassland? How will the associated changes in surface energy partitioning affect land-atmospheric feedbacks?

Hypotheses: A reduction in plant water availability will cause some tree mortality directly, but the main impact on forests will be seen in an increase in natural disturbance events (fire, insects), and changes in the composition of species that regenerate post-disturbance via changes in species recruitment and re-establishment.

SHIFTING WETLANDS

What we know: Peatlands play two critically important roles in the BPE: they act as sinks for water during wet periods and sources during dry periods; and they store and release C. Marshes, which are limited to the forest-grassland ecotone, have highly variable water levels that are sensitive to climate variability and occasionally dry out.

Knowledge gap: Will BPE peatlands remain stable under a changing climate? What will be their role in buffering hydrologic responses to climate change and variability? Will fens transition to more bog-like peatlands, together with the accompanying changes of acidity and vegetation? Will changes to peatlands and lakes result in changes in C sequestration in the BPE?

Hypotheses: With decreasing $P - E$, the marsh wetlands in the forest-grassland ecotone will retreat under increasing drought stress. The peatlands north of the forest-grassland ecotone will persist but will transition to lower water tables and more tree cover. Drying peatlands and warming lakes will lead to increased greenhouse emissions from the BPE.

Our hypotheses predict that changes in the BPE could result in significant loss of habitat, ecosystem services and carbon sequestration, and have a significant impact on regional climate. While the interaction between climate change and hydrology will affect the future potential vegetation distribution, we expect that actual changes in BPE vegetation
BOX 5

A WARMING WINTER

What we know: We can say with confidence that winter warming will occur, leading to less precipitation falling as snow, and smaller snow packs that melt earlier, combined with more rainfall.

Knowledge gap: How significant is snowmelt runoff over frozen soil on the overall partitioning of water between uplands and lowlands within the BPE? What are the controls on frozen soil infiltration capacity and how will they change? How do soil freezing and thawing affect transpiration? Will the decline in snowmelt runoff and the increase in growing-season rainfall satisfy the increased evaporative demands of a longer growing season?

Hypotheses: Climate change-driven winter warming will result in reduced snowfall, smaller snowpacks, reduced snowmelt runoff, increased rainfall and infiltration, more water available for evapotranspiration, more groundwater recharge, and more baseflow inputs to wetlands and streams. This will moderate the drying trend discussed above, but the net effect will be drying.

BOX 6

CLIMATE CHANGE AND WILDLIFE

What we know: Wildlife is impacted directly by changes in water availability, and indirectly by vegetative responses to climate change. Warmer, drier conditions will increase beaver abundance and distribution as well as increase insect outbreak frequency and intensity. Vegetation changes will reduce available forage for large ungulates, and reduce habitat availability for birds and other wildlife—including insectivorous birds that help keep insect outbreaks in check.

Knowledge gap: How will changes in wildlife populations cascade to affect other components of the ecosystem? In particular, how will populations of insects and insectivorous bird populations respond to change? How will beaver populations respond to change and what will be the cascading impacts on hydrology?

Hypotheses: Insectivorous birds will decrease in abundance across most of the BPE, contributing to the increased frequency and intensity of insect outbreaks and increased forest disturbance. The beaver population will densify in the interior of their range, which will offer peatland and riparian ecosystems enhanced resistance to change, while large ungulates will increasingly cluster around wetlands with high-quality forage thus increasing erosion rates.

will continue to be strongly influenced by human activities—particularly in southern regions. Human responses are likely to be decisive, and effective forest management strategies, such as fire suppression, intensive forest management, and replanting with drought- or pest-tolerant species, could have the potential to mitigate some of these changes.

Any predicted changes in the BPE are subject to high uncertainty, due to limited understanding of process interactions, and limitations in data. Climate, hydrological, and ecological monitoring activities in the BPE are limited, and may be inadequate to understand and predict the complex responses of the BPE to human activities and climate change. The path forward should include integrated observational programs and modeling activities to evaluate the suggested hypotheses and provide an improved understanding of the interacting responses of climate, hydrology, and ecology to climate change in the BPE. Particular modeling challenges include: Can we parameterize critical fine scale processes at coarser spatial scales, for use in climate and earth-system models? What degree of process complexity will be needed to capture the response of vegetation dynamics to climate change? Can we use a range of different types of observational data to better constrain our models and hence improve their predictive capacity? Are human activities (including land clearing for agriculture, logging, mining, fire suppression, tree planting, road building, seismic lines, hunting, and cottage building) predictable and could these effects be included in the earth systems models for the assessment of associated eco-hydrological change?

The case study of the BPE raises fundamental challenges of global relevance in terms of predicting responses of complex earth systems to changing moisture and temperature regimes, in particular in the transitional areas that are particularly vulnerable to shifting climate, land-cover, and hydrology.
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