AGU PUBLICATIONS
JGR
Journal of Geophysical Research: Biogeosciences

REVIEW
10.1002/2015JG003133

Special Section:
Arctic Freshwater Synthesis

Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime

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Key Points:

- Changes in the Arctic freshwater sources, fluxes and storage have profound implications for ecosystems
- Significant uncertainty remains in forecasting impacts on ecosystem properties and processes
- Enhanced circumpolar catchment-scale research efforts are needed to reduce uncertainties

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Citation:
Wrona, F. J., M. Johansson, J. M. Culp, A. Jenkins, J. Mård, I. H. Myers-Smith, T. D. Prowse, W. F. Vincent, and P. A. Wookey (2016), Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime, *J. Geophys. Res. Biogeosci.*, *121*, 650–674, doi:10.1002/2015JG003133.

Received 13 JUL 2015
Accepted 4 MAR 2016
Accepted article online 8 MAR 2016
Published online 30 MAR 2016

Abstract Numerous international scientific assessments and related articles have, during the last decade, described the observed and potential impacts of climate change as well as other related environmental stressors on Arctic ecosystems. There is increasing recognition that observed and projected changes in freshwater sources, fluxes, and storage will have profound implications for the physical, biogeochemical, biological, and ecological processes and properties of Arctic terrestrial and freshwater ecosystems. However, a significant level of uncertainty remains in relation to forecasting the impacts of an intensified hydrological regime and related cryospheric change on ecosystem structure and function. As the terrestrial and freshwater ecology component of the Arctic Freshwater Synthesis, we review these uncertainties and recommend enhanced coordinated circumpolar research and monitoring efforts to improve quantification and prediction of how an altered hydrological regime influences local, regional, and circumpolar-level responses in terrestrial and freshwater systems. Specifically, we evaluate (i) changes in ecosystem productivity; (ii) alterations in ecosystem-level biogeochemical cycling and chemical transport; (iii) altered landscapes, successional trajectories, and creation of new habitats; (iv) altered seasonality and phenological mismatches; and (v) gains or losses of species and associated trophic interactions. We emphasize the need for developing a process-based understanding of interecosystem interactions, along with improved predictive models. We recommend enhanced use of the catchment scale as an integrated unit of study, thereby more explicitly considering the physical, chemical, and ecological processes and fluxes across a full freshwater continuum in a geographic region and spatial range of hydroecological units (e.g., stream-pond-lake-river-near shore marine environments).

1. Introduction

Successive international scientific assessments and related journal articles have described the observed and potential impacts of global and regional climate variability and change, and other related environmental stressors, on Arctic terrestrial and freshwater ecosystems [e.g., *ACIA*, 2005; *SWIPA*, 2011; *ABA*, 2013; *Jeffries et al.*, 2014; *Larsen et al.*, 2014]. Correspondingly, there is a growing recognition that observed and projected changes in the magnitude and variability in the hydrologic regimes in the Arctic have, and will have, increasingly profound implications for associated physical, geochemical, biological, and ecological properties and processes in terrestrial, freshwater, and marine ecosystems [*White et al.*, 2007; *Callaghan et al.*, 2013; *Ims et al.*, 2013; *Wrona et al.*, 2013; *Bring et al.*, 2016; *Carmack et al.*, 2016; *Lique et al.*, 2016; *Prowse et al.*, 2006a, 2006b, 2011, 2015a, 2015b; *Vihma et al.*, 2016].

An intensified hydrological cycle in the Arctic [*Peterson et al.*, 2002; *Déry et al.*, 2009; *Fichot et al.*, 2013; *Rawlins et al.*, 2010; *Zhang et al.*, 2013a], together with changes in the cryosphere (e.g., increasing active layer depth and changes to the extent and magnitude of permafrost thaw) [*Oelke et al.*, 2004; *Zhang et al.*, 2005; *Harden et al.*, 2012; *Shiklomanov et al.*, 2010, 2013], will have fundamental consequences for water flow volumes, timing, and pathways through terrestrial ecosystems [*Frey et al.*, 2007; *Frampton et al.*, 2013; *Jantze et al.*, 2013; *Karlsson et al.*, 2015]. Other ecosystem effects include alterations in the storage and cycling of freshwater on the landscape, increases in thermokarst slumping events and related sediment transport, and changes in the timing, duration, and quality of lake and river ice cover [*White et al.*, 2007; *Rawlins et al.*, 2010; *Prowse et al.*, 2011; *Callaghan et al.*, 2013; *Wrona et al.*, 2013; *Bring et al.*, 2016].

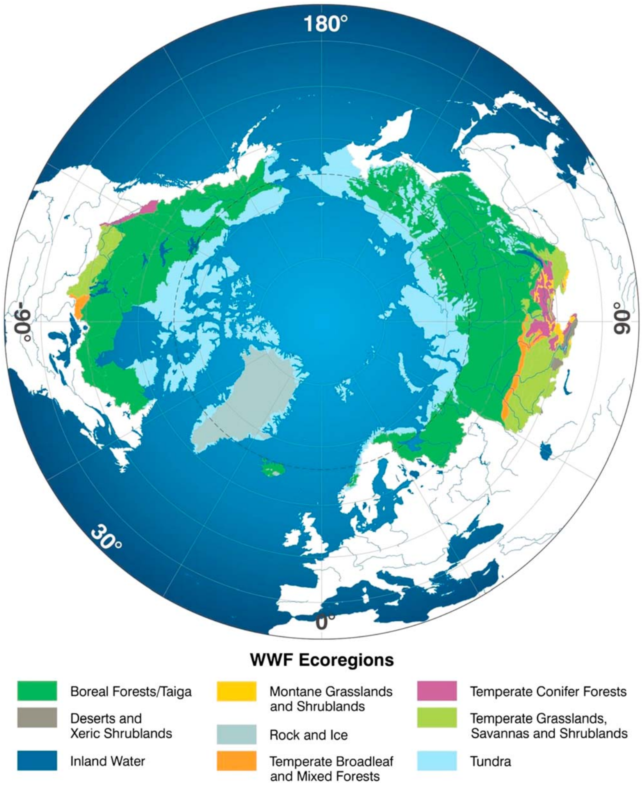

Figure 1. Distribution of major World Wildlife Fund ecoregions in the Arctic [from *Prowse et al.*, 2015a].

Although significant progress has been made over the past decade in climate modeling and related global and regional climate projections [*Lique et al.*, 2016], a major source of uncertainty for predicting ecological impacts is understanding the extent and magnitude of hydrological and climate-related change that microorganisms, plants, animals, and ecosystems will undergo in the coming decades [*Blois et al.*, 2013; *Diffenbaugh and Field*, 2013; *Bring et al.*, 2016; *Prowse et al.*, 2015a]. Given the projected regional variability in the Arctic, and associated alterations in the magnitude, duration, and geographic extent of hydrologic extremes, new information is needed to assess the effects of future changes in ecologically critical hydroclimatic conditions and regions on species distribution and abundance patterns and related biodiversity, impacts on ecosystem processes and function, and related provisions of ecosystem services. Such information will be essential for the development and implementation of suitable adaptation, conservation, and management actions for terrestrial and freshwater biota and related ecosystems [*Azcárate et al.*, 2013; *Ims et al.*, 2013; *Wrona et al.*, 2013; *Bring and Destouni*, 2014].

The goal of this paper is to conduct a high-level synthesis of the observed and projected implications of a changing and intensifying Arctic hydrological regime in its various states (i.e., liquid water, snow, ice, permafrost) on key geochemical, biological, and ecological properties of terrestrial and freshwater ecosystems. The paper is the terrestrial ecology contribution to a broader Arctic Freshwater Synthesis (for an overview, see *Prowse et al*. [2015a]), which is an interdisciplinary and integrated effort to review the current state of knowledge, identify key knowledge gaps, highlight areas of uncertainty, and suggest broad-themed priority areas that need to be addressed through enhanced integrated research and monitoring efforts.

2. Alterations in Arctic Hydrology: Implications for Terrestrial and Freshwater Ecosystems

The Arctic encompasses a broad range of geographical and ecological conditions with river, lake, pond, and wetland complexes providing a key linkage across landscapes and environmental gradients. A range of terrestrial vegetation zones exist in the Arctic, typified by the dominant vegetation types that occur with increasing latitude, the occurrence of continuous versus discontinuous permafrost, total degree days available for growth, and the duration of snow and ice cover (Figure 1, from *Prowse et al.* [2015a]). There is a continuous gradient of environmental severity within the Arctic, from the boreal forest zone at its southern boundary to the open tundra and polar deserts of the far north, and along this gradient, freshwater ecosystems are prevalent [*Vincent and Laybourn-Parry*, 2008]. The nature of the dominant vegetation changes from erect woody plants to low-growing herbs to mosses, lichens, and polar desert crusts, and the complexity of the canopy in horizontal and vertical dimensions decreases from south to north [*Callaghan et al.*, 2011; *Ims* *et al*., 2013; *Walker et al*., 2005]. In addition, the Arctic tundra biome is strongly influenced by coastal maritime climatic and hydrological regimes, with 80% of the lowland areas occurring within 100 km of seasonally ice-covered oceans [*AMAP*, 2011; *Ims et al*., 2013]. Thus, though temperature is a key driver of ecological processes in tundra ecosystems, it is hydrological interactions that mediate the climate responses of tundra ecosystems.

Commensurate with the range of terrestrial ecosystems described above, a great variety of freshwater ecosystem types occur in the Arctic [*Huryn et al*., 2005; *Vincent and Laybourn-Parry*, 2008; *Moss et al*., 2009; *White et al*., 2007; *Wrona et al*., 2013]. Freshwater systems often form a continuum, ranging from ephemeral shallow ponds to large lakes, small intermittent streams to more permanently flowing large rivers, and intricate wetland complexes composed of fens, bogs, and marshes [*Vincent and Laybourn-Parry*, 2008]. In northern latitudes, hydrological processes and, as such, associated freshwater ecosystems are controlled by the local and regional catchment characteristics, such as geology and landscape geomorphology, the associated terrestrial vegetation cover, and the presence or absence of permafrost [*White et al*., 2007]. Collectively, these attributes affect the physical and geochemical properties of freshwater environments and their related habitat quality and quantity. Since freshwater ecosystems form an often highly interconnected network at the landscape scale, they serve as important integrators of hydrological, atmospheric, and terrestrial processes [*Schindler*, 2009; *Williamson et al*., 2008, 2009].

Hence, changes in hydrological regimes through alterations in precipitation, evapotranspiration (ET), and runoff and associated changes in the spatial and temporal distribution and properties of snow, ice, and permafrost collectively have significant implications on the types, biogeography, and associated ecological structure and function of Arctic ecosystems and related biota [see *Bring et al*., 2016; *Callaghan et al*., 2004a, 2004b, 2011; *Hinzman et al*., 2005; *Peterson et al*., 2006; *White et al*., 2007; *Rawlins et al*., 2010; *Ims et al*., 2013; *Prowse*, 2012; *Prowse et al*., 2011, 2015a, 2015b; *Vincent et al*., 2011; *Jeppesen et al*., 2013; *Lique et al*., 2016; *Vihma et al*., 2016; *Wrona et al*., 2006a, 2006b, 2013].

Below we discuss five prominent ecosystem attributes and processes that will be directly or indirectly affected through local, regional, and circumpolar changes in associated hydrologic regimes. These include (i) changes in ecosystem productivity; (ii) alterations in ecosystem biophysical properties, biogeochemical cycling, and chemical transport; (iii) altered landscapes, successional trajectories, and creation of new habitats; (iv) altered seasonality and phenological mismatches; and (v) gains or losses of species and implications on trophic interactions.

2.1. Changes in Ecosystem Productivity

An altered hydrological regime has important implications for the present and projected productivity of terrestrial and freshwater ecosystems. Autotrophic and heterotrophic productivity in Arctic ecosystems is limited primarily by abiotic factors such as temperature and photoperiod, and also by bottom-up hydrological and ecological processes that affect nutrient availability (e.g., phosphorus, nitrogen, carbon) and biotic interactions [*Ims et al*., 2013; *Wrona et al*., 2013].

Changes in Arctic terrestrial productivity have been linked to warming, moisture regime, and disturbance (e.g., permafrost disturbances [*Epstein et al*., 2012; *Frost et al*., 2013], fire [*Lantz et al*., 2010], and changing herbivore pressure [*Olofsson et al*., 2009; *Speed et al*., 2010; *Kerby and Post*, 2013a, 2013b]). From a hydrological and climatic perspective, shifts in plant productivity are driven in part by changes in seasonality (e.g., snowmelt, growing season length, and freezeup [*Xu et al*., 2013]) and in the thermal and precipitation regimes (e.g., leading to warming, changes in soil moisture, and extreme events such as drought, floods, and thawing and freezing events [*Bokhorst et al*., 2011; *Elmendorf et al*., 2012]). Increasing permafrost thaw can alter hydrology [*Jorgenson et al*., 2013], landscape integrity [*Hinzman et al*., 2005; *Jorgenson et al*., 2006], soil nutrient availability [*Natali et al*., 2013; *Pizano et al*., 2014], and resulting biological activity [*Natali et al*., 2012]. Changes in the water holding capacity and drainage of soils can also affect terrestrial productivity and ecosystem function [*Seneviratne et al*., 2010; *Ims et al*., 2013].

Satellite observations indicate an increase in terrestrial productivity, commonly referred to as the greening of the Arctic [*Jia et al*., 2003, 2009; *Forbes et al*., 2010; *Beck and Goetz*, 2011; *Walker et al*., 2012; *Macias-Fauria et al*., 2012; *Gamon et al*., 2013; *Guay et al*., 2014; *Urban et al*., 2014]. These changes have been detected by a comparison of repeat photographic images at specific locations [e.g., *Tape et al*., 2006], by comparisons with earlier vegetation plot and transect analyses [e.g., *Hill and Henry*, 2010; *Elmendorf et al*., 2012], and by time series analysis of satellite data, notably the normalized difference vegetation index (NDVI) [e.g., *Gamon et al.*, 2013; *Xu et al.*, 2013]. Questions remain, however, on whether changes in the NDVI signal (which is a proxy) represent true increases in primary productivity on the landscape. Since most long-term NDVI data sets are from multiple sensor systems, lack of correspondence between different satellite systems introduces substantial uncertainties in attributing trends to changing productivity on the ground [*Guay et al.*, 2014; *Tian et al.*, 2015]. Some of the most prominent examples of increased productivity in terrestrial environments include the widespread increases in shrub abundance and biomass reported at sites around the tundra biome [*Sturm et al.*, 2001; *Tape et al.*, 2006; *Myers-Smith et al.*, 2011; *Elmendorf et al.*, 2012].

As climate warms, the amount of riparian vegetation along Arctic aquatic systems is also predicted to increase due to the process referred to as shrubification [*Myers-Smith et al.*, 2011]. A higher biomass of terrestrial vegetation in the riparian zone of freshwater systems would be expected to raise the input of terrestrial carbon to adjacent waters. An increase in riparian input from shrubs (e.g., birch, willow, and alder: *Betula*, *Salix*, and *Alnus* spp., respectively) would provide energy supplements to lotic and lentic food webs (i.e., both dissolved and particulate organic matter) that would be available to, and correspondingly increase production of, microbial decomposers and invertebrate detritivores (i.e., insect shredders and collectors) [*Wrona et al.*, 2013]. In addition, nitrogen-fixing alders could bring additional nitrogen into terrestrial, riparian, and aquatic systems [*Tape et al.*, 2006]. However, increases in the concentrations and loadings of dissolved organic carbon can also negatively affect autotrophic production through increased water column light inhibition (see discussion below on aquatic browning).

Enhanced nutrient fluxes from land to water, resulting from a deepening of the soil active layer and increased thermokarst activity, have been associated with increasing water column ion and nutrient concentrations, leading to enhanced autotrophic productivity in freshwater ecosystems (referred to as aquatic greening) [e.g., *Hessen et al.*, 2004; *Smol et al.*, 2005; *Kokelj et al.*, 2005; *Lantz and Kokelj*, 2008; *Bowden et al.*, 2008; *Keller et al.*, 2010; *Thompson et al.*, 2012; *Thienpont et al.*, 2013]. Decreasing ice cover thickness and duration [e.g., *Magnuson et al.*, 2000; *Duguay et al.*, 2006; *Wrona et al.*, 2013; *Surdu et al.*, 2014; *Paquette et al.*, 2015] have also been documented in Arctic freshwater ecosystems and may contribute to increased phytoplankton production and a shift in the partitioning of photosynthesis between the water column and benthic phototrophic communities [*Vadeboncoeur et al.*, 2003]. Additional enhanced primary productivity may occur through the increased growth of aquatic plants, and the gradual infilling of ponds [*Andresen and Lougheed*, 2015] and the increase in riparian vegetation [*Tape et al.*, 2015]. However, the magnitude, pace, and regional variability of each of these productivity changes remain poorly known.

Another key process affecting the phototrophs as well as microbial heterotrophs occurs with the landscape inputs of allochthonous colored dissolved organic matter (CDOM) and associated dissolved organic carbon (DOC) arising from enhanced mobilization from terrestrial landscapes and wetlands related to increased air temperature, precipitation, and permafrost thaw [*Hessen et al.*, 2008; *Wrona et al.*, 2006a; *Rautio et al.*, 2011; *Vonk et al.*, 2015; *Bring et al.*, 2016]. The browning of water arising from elevated levels of dissolved organic matter has been observed in many northern temperate and Arctic freshwater ecosystems [e.g., *Karlsson et al.*, 2001; *Jorgenson et al.*, 2001; *Kokelj et al.*, 2005, 2009; *Hessen et al.*, 2004; *Roulet and Moore*, 2006; *Rautio et al.*, 2011; *Thompson et al.*, 2012; *Vonk and Gustafsson*, 2013; *Tanentzap et al.*, 2014]. Consequently, the optical conditions of aquatic systems are strongly influenced by the concentrations of terrestrially derived CDOM, which in turn controls the attenuation of short-visible and ultraviolet (UV) radiation and thereby the relative productivity of water column versus benthic communities [*Laurion et al.*, 1997; *Gareis et al.*, 2010; *Pienitz and Vincent*, 2000; *Rautio et al.*, 2011; *Watanabe et al.*, 2011; *Wrona et al.*, 2006b]. Thus, alterations in the transport, distribution, concentrations, and optical properties of dissolved organic matter in Arctic freshwaters will affect phototrophic and microbial diversity and productivity, with cascading effects on the aquatic food web structure [*Hessen et al.*, 2004; *Vincent and Laybourn-Parry*, 2008; *Sweetman et al.*, 2010; *Rautio et al.*, 2011; *Hobbie and Kling*, 2014; *Wrona et al.*, 2006a, 2006b, 2013]. Changing CDOM conditions will also alter the photochemical priming of bacterial production [*Cory et al.*, 2014], in addition to the direct effects of changes in DOC concentration and lability on microbial heterotrophs.

At a catchment scale, increased precipitation and resulting runoff may accelerate permafrost thawing, weathering, soil/sediment erosion, and nutrient loading into rivers and lakes, thereby contributing to enhanced autotrophic and heterotrophic productivity of aquatic systems [e.g., *Kokelj et al.*, 2013, 2015; *Nilsson et al.*, 2015]. *Kokelj et al.* [2013] observed mass wasting of valley slopes in the Peel River watershed, northwest Canada, which increased rapidly during an extremely wet summer, leading to increased delivery of both nutrients and suspended sediments to surface waters. Thus, increased precipitation may lead to aquatic greening or browning depending on the magnitude of increase in nutrient and sediment drivers of ecological change. In addition, future increases in runoff will not only flush more organic matter from catchments into streams and rivers but may also affect iron (Fe) concentrations which in turn influence the degree of CDOM-related browning as a result of strong light absorption by organic carbon-Fe complexes [*Weyhenmeyer et al*., 2014].

Changes in snow and ice cover on freshwater and terrestrial systems are additional hydrologic drivers that are codriven by air temperature and that directly affect under snow and ice biological production [*Callaghan et al*., 2011; *Prowse et al*., 2011; *Vincent et al*., 2013]. Effects are projected to occur at the individual level (e.g., displacement from preferred habitat and alteration in growth rates), the population level (e.g., changes in distribution and range and abundance), and community/trophic levels (e.g., especially destabilization of predator-prey dynamics [*Nelson et al*., 2006]). Increasing snow cover over ice reduces the availability of light for photosynthesis and may impair the growth of aquatic mosses [*Riis et al*., 2014] and other benthic communities [*Wrona et al*., 2013]. A paleolimnological study on Lake El'gygytgyn, an ancient crater lake in the Siberian Arctic, found that periods of the highest primary productivity were associated with warm, ice-free summer conditions, while the lowest rates were coincident with periods of perennial ice [*Melles et al*., 2007]. While snow-free ice conditions are known to promote bloom concentrations of photosynthetic flagellates, lake under-ice plankton abundance could be negatively affected by the projected increases in surface accumulations of snow and the formation of white ice which impairs light penetration to the waters beneath [*Wrona et al*., 2006a, 2006b; *Vincent and Laybourn-Parry*, 2008]. Such changes in snow and white-ice coverage are also likely to affect levels of secondary productivity such as in zooplankton and fish [*Borgstrøm and Museth*, 2005; *Prowse et al*., 2006a]. However, these effects may be offset by a decreased duration of ice cover with climate warming, with improved light environments and increased mixing of nutrients throughout the water column during open-water conditions [*Veillette et al*., 2011].

Rivers are unique freshwater environments since the biological productivity of these ecosystems is tightly linked to material input from terrestrial landscapes [*Vannote et al*., 1980]. These terrestrial materials include surface and groundwater inputs that create river flow, dissolved nutrients that promote primary production, allochthonous organic matter from terrestrial vegetation and soils (discussed above), and land-derived sediments that can be nutrient sources as well as modifiers of the physical habitat (i.e., the streambed substrate). In Arctic rivers, it is the shift in the source and quantity of this input of terrestrial material that will likely be an important effect of climate change on river food web productivity and composition. Although changes in the ecological structure, function, and related productivity of these river ecosystems are expected [*Prowse et al*., 2006a; *Wrona et al*., 2006a; *Vincent et al*., 2011], the exact shifts are difficult to predict because these changes will vary along complex environmental gradients related to stream order (i.e., small, low-order to larger, high-order systems), subarctic to high-Arctic latitudes, and terrestrial topography (i.e., low- to high-slope landscapes).

2.2. Alterations in Biophysical Properties, Biogeochemical Cycles, and Chemical Transport

Changes in precipitation, seasonal snow and ice cover, permafrost dynamics, fire, and vegetation structure will influence the rates and magnitudes of nutrient cycling and export, influence the release and transport of bound or deposited contaminants, and alter biophysical properties such as successional patterns of both terrestrial and freshwater ecosystems [*SWIPA*, 2011; *Ims et al*., 2013; *Wrona et al*., 2013; *Bring et al*., 2016].

An intensified hydrological cycle, together with changes in the cryosphere (e.g., increasing active layer depth), will influence soil and sediment moisture and thermal regimes [*Iijima et al*., 2010; *Mcclymont et al*., 2013], and redox status [*Lipson et al*., 2015], differentially in contrasting landscape contexts, with implications for net primary productivity (section 2.1), decomposition [*Hugelius et al*., 2012; *Yi et al*., 2014], and fermentative processes [*Schuur et al*., 2008; *Nowinski et al*., 2010]. The consequence for net greenhouse gas emissions, the relative contribution of CO_2 and CH_4, and the delivery of organic and inorganic materials to surface waters will be profound [*Verville et al*., 1998; *Kokelj et al*., 2009; *Mazeas et al*., 2009; *Jantze et al*., 2013; *Christensen*, 2014; *Olefeldt et al*., 2014; *Serrano-Silva et al*., 2014].

Changes to biogeochemical cycling can occur from changes in hydrology and resulting ecological communities. Striking examples of changes in hydrology in relation to permafrost warming and thawing include shifts from dry and mesic soils and vegetation communities to wetland communities [*Osterkamp et al.*, 2000; *Camill*, 2005; *Karlsson et al.*, 2011; *McClymont et al.*, 2013; *Quinton and Baltzer*, 2013; *Baltzer et al.*, 2014] and, conversely, from wet ice wedge polygonal tundra to drier, mesic conditions [*Perreault et al.*, 2015]. Such changes in hydrology are associated with fundamental shifts in greenhouse gas emissions related to soil and sediment redox status and vegetation change [*Moore et al.*, 1998; *Olefeldt et al.*, 2014; *Hodgkins et al.*, 2014]. Peat plateau and lake margin areas are notable for the very large carbon stocks which may now be vulnerable to loss to the atmosphere and surface waters as a consequence of permafrost thaw and thermokarst [*Olefeldt and Roulet*, 2012; *Hugelius et al.*, 2013].

A warming climate can cause either increased thermokarst, resulting in lake formation, or increased drainage as the permafrost thaws [*Sannel and Kuhry*, 2011; *Karlsson et al.*, 2014; *Perreault et al.*, 2015] (see section 2.3). Both processes are currently being observed in the Arctic, with the magnitude of each depending on the geographic location [*Vincent et al.*, 2011]. Based on the limited evidence available to date, the decadal dynamics of these transformations appear most pronounced in the sporadic permafrost zone, but it can be anticipated that this will extend increasingly into the (current) discontinuous zone, with implications for hydrology and carbon cycling. Changing soil moisture conditions associated with permafrost thaw and alterations in soil moisture, permafrost collapse after shrub removal, and the occurrence extent of ponds and lake have been demonstrated to be key drivers of CO_2 and CH_4 release [*Natali et al.*, 2015; *Nauta et al.*, 2015; *Olefeldt et al.*, 2013; *Abnizova et al.*, 2012].

In permafrost landscapes, the complex interactions among topography, water, soil, vegetation, and snow [*Woo et al.*, 2007; *Jorgenson et al.*, 2010; *Zhang et al.*, 2013b; *Gangodagamage et al.*, 2014], which are referred to subsequently as ecohydrogeomorphic, represent unique challenges for the scientific community. Cascading effects of change in any one individual system component in response to global change or land management drivers can interact with other components, often spanning contrasting temporal and spatial scales [*Shaver et al.*, 2000; *Wookey et al.*, 2009]. One example of this would be the shift in vegetation from dwarf and low-shrub tundra communities to higher-stature shrub communities in response to warming (Figure 2) [*Myers-Smith*, 2007; *Myers-Smith et al.*, 2011], which influences snow drifting patterns, albedo, transpiration, soil thermal and moisture regimes, and active layer thickness [*Sturm et al.*, 2005a, 2005b; *Helama et al.*, 2011; *Loranty et al.*, 2011; *Gangodagamage et al.*, 2014]. Furthermore, a shift in vegetation type will also influence belowground processes (e.g., organic matter decomposition, CO_2, CH_4, and dissolved organic matter release) through changes in rhizosphere processes and mycorrhizal associations [*Lindahl and Tunlid*, 2015]; however, these changes may not result in changes to soil carbon storage [*Sistla et al.*, 2013]. Taken together, these ecohydrogeomorphic processes will profoundly influence the delivery of organic and inorganic materials to subsurface and surface waters, but they are responding to a suite of abiotic and biotic drivers of change, which are difficult to tease apart.

Particularly in Arctic first-order headwater catchments [*Denfeld et al.*, 2013], the transition from soil water to surface water results in rapid loss of dissolved CO_2 and CH_4 as a result of the process of evasion, which until recently has been neglected in landscape carbon budgets, especially in tundra environments [*Kling et al.*, 1991; *Tank et al.*, 2012a, 2012b]. However, delivery of particulate and dissolved organic matter from the terrestrial realm to surface waters, via subsurface flow and/or surface wash, is also a key flux where downstream biological and photochemical processing may continue over distances extending from local to regional scales [*Cory et al.*, 2014], including into the marine environment [*Bélanger et al.*, 2006; *Vallières et al.*, 2008; *Selver et al.*, 2012; *Feng et al.*, 2013] and sometimes via deltaic systems. Evidence is also mounting, through radiocarbon measurements of particulate and dissolved organic carbon (including specific molecular soil markers), of a permafrost thaw-induced mobilization of old soil and sediment organic matter into surface waters in the Arctic [*Guo et al.*, 2007; *Gustafsson et al.*, 2011; *Lamoureux and Lafreniere*, 2014; *Mann et al.*, 2015]. It is not, however, currently easy to ascribe its source [*Taylor and Harvey*, 2011; *Feng et al.*, 2013], whether from direct fluvial erosion of riverbanks or via subsurface and surface pathways through and across terrestrial landscapes.

The downstream fate of two key contrasting Arctic organic matter pools (a young surface peat component and an old, deep mineral soil-associated component) contrasts dramatically [*Vonk et al.*, 2010]. The young pool comprises an easily degradable humic suspension, while the old pool preferentially settles to sediments

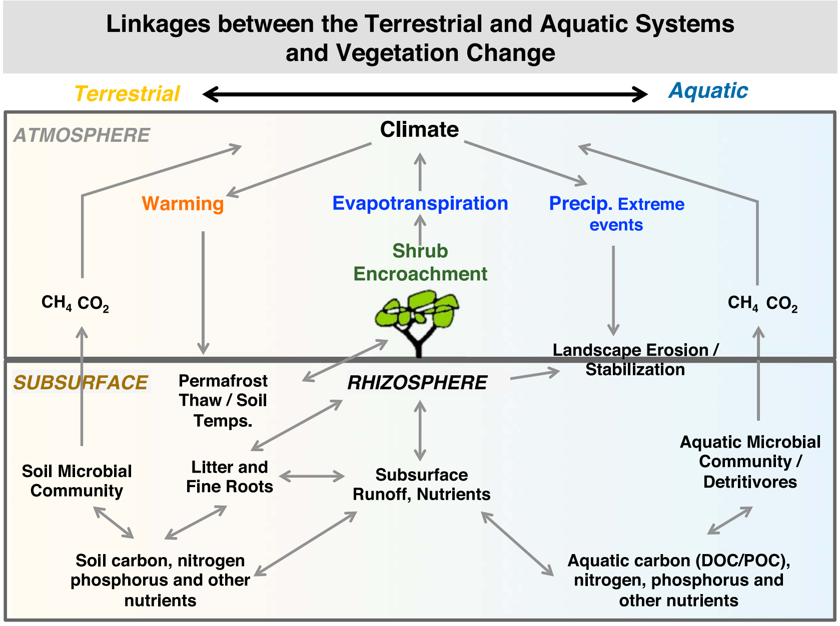

Figure 2. Linkages and possible effects of vegetation change on Arctic terrestrial and aquatic biogeochemical and ecological processes. Increases in shrub species could lead to enhanced litter and fine root inputs and nitrogen fixation in terrestrial soils, thereby altering nutrient cycling and leading to greater runoff into aquatic systems [*DeMarco et al.*, 2014; *Stewart et al.*, 2014]. Furthermore, proliferation of shrubs may influence evapotranspiration rates and the stability of stream banks, pond, and lake shores [*Tape et al.*, 2011; *Pearson et al.*, 2013]. In contrast, removal of shrub canopies can lead to permafrost thaw and the transition of ecosystems from terrestrial to aquatic [*Blok et al.*, 2010; *Myers-Smith and Hik*, 2013]. Collectively, these ecological feedbacks of vegetation change can influence inputs of nutrients and fluxes of gaseous, particulate (POC) and dissolved organic carbon (DOC), potentially leading to enhanced productivity across both terrestrial and aquatic Arctic ecosystems [adapted from *Myers-Smith et al.*, 2011].

by being both physically protected from degradation and ballasted (by the mineral matrix) for sedimentation. In short, the former (peat-derived) organic matter has the potential to rapidly add greenhouse gases to the atmosphere. Placed into a broader context, this return of terrestrially derived carbon to the atmosphere, via surface waters, supplements direct land-atmosphere fluxes. Natural abundance radiocarbon and $\delta^{13}C$ analysis of respired CO_2 from soils in areas of thawing permafrost also indicates potential mobilization of the old soil carbon [*Schuur et al.*, 2009; *Hicks Pries et al.*, 2013].

Increased terrestrial productivity (as described in section 2.1) in boreal forest, subarctic, and Arctic tundra regions can be expected to have significant downstream consequences for biogeochemical exports to the ocean [*Carmack et al.*, 2016]. Based on the current state of knowledge, however, it is really only possible to speculate on these potential (or actual) effects, partly because interacting ecohydrogeomorphic factors do not enable simple causality to be established. Arctic greening is likely to be strongly linked to substrate conditions (including hydrology and cryoturbation) at the landscape scale [*Elmendorf et al.*, 2012; *Macias-Fauria et al.*, 2012; *Frost et al.*, 2014], further complicating the interpretation of potential effects on surface waters.

Several ecological mechanisms and processes could be related to the effects of increased productivity of existing vegetation and resulting alterations in biogeochemical fluxes and cycling (Figure 2). These include, for example, (i) altered rates and magnitudes of transpiration (and hence water balance and chemical transport), (ii) altered root and mycorrhizal biomass and metabolism (potentially affecting DOC and dissolved inorganic carbon concentrations in soil water and delivery to surface waters), (iii) demand for mineral nutrients (and hence soil chemistry), and (iv) direct effects of riparian vegetation on surface water thermal and light regimes, as well as the delivery of particulate organic matter (e.g., leaf litter) directly to surface waters.

Arctic rivers are generally nutrient poor (oligotrophic), with autochthonous primary production being limited both by low P and N concentrations [*Milner et al.*, 2005, 2009; *Lento et al.*, 2013] and by light availability [*Vallières et al.*, 2008]. Future nutrient concentrations in Arctic freshwater ecosystems are predicted to increase as a result of climate warming and the resultant increased nutrient loading from thawing permafrost

[*Rouse et al*., 1997; *Bowden et al*., 2008; *Kokelj et al*., 2013], particularly if this is not accompanied by sedimentation [*Bowden et al*., 2012]. In nutrient-poor Arctic streams, increased nutrient loading is expected to raise autochthonous production and alter algal community composition [*White et al*., 2007]. Following the River Continuum Concept [*Vannote et al*., 1980], the greatest effect is expected in low- to mid-order rivers, where turbidity regimes are reduced compared to higher-order systems, thereby allowing ample light for primary production during the ice-free period.

The greening of river ecosystems through increased autochthonous production is projected to be most pronounced in low-Arctic environments, which are expected to warm earlier in the spring and summer seasons than high-Arctic systems. Moreover, the water budget and nutrient sediment supply of cold region delta riparian zones are heavily dependent on ice jam floodwaters. Studies of the Mackenzie River Delta riparian lake system (approximately 45 000 in number), whose highest flood stages are dependent on ice jams [*Goulding et al*., 2009], indicate that decreases in the severity of river ice breakup have lessened the flooding of the high-closure lakes and the biogeochemical processing of river water upon which the ecological health of this extensive, floodplain ecosystem depends [*Lesack and Marsh*, 2007].

In addition to carbon/nitrogen and other nutrient elements and their responses to changes in hydrological and related codrivers, contaminants (e.g., mercury and persistent organic pollutants) may also be mobilized from terrestrial ecosystems and freshwater sediments [*AMAP*, 2011; *Macdonald et al*., 2005; *Wrona et al*., 2006a; *Outridge et al*., 2007; *Stern and Lockhart*, 2009; *Carrie et al*., 2010; *Stern et al*., 2012; *MacMillan et al*., 2015]. An intensified hydrological cycle along with other climate-induced changes (i.e., increasing temperatures, permafrost thaw, and altered snow regimes) is projected to alter the fate, distribution, and uptake of contaminants in terrestrial and aquatic food webs [*AMAP*, 2003; *ACIA*, 2005; *Macdonald et al*., 2005; *Stern and Lockhart*, 2009; *Callaghan et al*., 2011; *Stern et al*., 2012]. For example, alterations in water discharge regimes have been shown to have an amplifying effect on particulate mercury flux in the Mackenzie River, Canada [*Leitch et al*., 2007]. *MacMillan et al*. [2015] found elevated water methylmercury concentrations in thaw ponds were highly correlated with variables associated with high inputs of organic matter, nutrients, and microbial activity. They further postulated that enhanced hydrological connectivity from thawing permafrost could enhance transport of mercury from thaw ponds to neighboring aquatic ecosystems. *Veillette et al*. [2012] found perfluorinated chemicals (PFCs), transported to the Arctic via long-range atmospheric processes, entered far northern catchments on Ellesmere Island, Nunavut, Canada, via the snowpack, inflowing streams, and lake water. They further projected that altered hydrologic regimes and lake ice cover in response to climate warming will have significant implications for the distribution, transport, and retention of PFCs in Arctic catchments and loadings to the ocean.

One of the strongest ecological effects of the projected change to lake ice regimes is alterations to lake thermal structure [*Bring et al*., 2016]. Of particular note is that high-latitude lakes along a 105°W transect (continental North America) exhibited less projected change in summer stratification than those along 90°E (continental Asia) [*Dibike et al*., 2011]; the differences are possibly due to regional contrasts in warming and/or differences in relative coldness. In a warming Arctic, shallower lakes that are not thermally stratified will have greater opportunity for mixing surface waters with sediments, resulting in greater carbon recycling within the water column. In contrast, organic particles sinking below the thermocline in thermally stratified lakes may not return to surface waters until fall turnover, decreasing the likelihood of carbon lost to sedimentation being recycled back into the water column [*Flanagan et al*., 2006].

Alterations in the timing and duration of ice cover can also affect the distribution and fate of contaminants in freshwater systems. Greater methylation of mercury, for example, is likely to result from higher temperatures, particularly in shallow zones [*Outridge et al*., 2007]. Moreover, higher water temperature is likely to increase pelagic production and thereby enhance algal scavenging of mercury, which is a pathway by which mercury can enter lentic food webs [*Outridge et al*., 2007]. Higher surface water temperatures associated with a decrease in ice cover, and related changes in food and energy pathways and/or productivity (benthic to pelagic), will likely modify the movement of contaminants through such systems [*Carrie et al*., 2010].

Climate change is likely to affect the physical and biogeochemical processes that control methane emissions from northern lakes, rivers, and wetlands. From culture studies to ecosystem measurements, methanogenesis has been shown to be highly responsive to temperature, implying that climate warming will accelerate methane production at a global scale [*Yvon-Durocher et al*., 2014; *Walter et al*., 2007, 2008; *Laurion et al*., 2010]. Such effects have been observed in northern studies; for example, laboratory warming of peat samples from a Siberian mire resulted in higher rates of methane production [*Metje and Frenzel*, 2007], implying that longer ice-free conditions in northern wetlands could lead to increased methanogenesis. However, the net emission of methane is also determined by the rates of methane consumption by methanotrophs. For example, bacterial communities of subarctic thermokarst ponds contain a high proportional abundance of methanotrophs [*Crevecoeur et al.*, 2015], and anaerobic methane oxidation may also take place in high-latitude lake sediments and wetlands [*Stoeva et al.*, 2014]. Much uncertainty still remains regarding what changes in environmental factors, alone or in combination, affect the relative balance of methanogenesis and methanotrophy [*Walter et al.*, 2007, 2008; *Laurion et al.*, 2010]. The prolonged winter ice cover over thermokarst lakes can result in full water column anoxia, which is conducive to methanogenesis [*Deshpande et al.*, 2015], and reductions in this ice cover may allow longer periods of methane oxidation. However, the importance of subice methane oxidation processes has not been assessed to date. Lake sediment warming experiments indicate that higher temperatures may stimulate methanogenesis to a greater extent than methanotrophy [*Duc et al.*, 2010]. These results imply that warmer littoral sediments under longer ice-free conditions may have higher rates of net methane emission; conversely, if the offshore waters become more strongly stratified under a warmer climate, the hypolimnion and deeper sediments may experience cooler conditions [e.g., *Livingstone and Lotter*, 1998] that would likely inhibit net methane production.

Climate change may also affect carbon burial rates in northern freshwater ecosystems. Based on a broad range of six climate warming scenarios from the Intergovernmental Panel on Climate Change [*Solomon et al.*, 2007], it is projected that there will be a 4–27% decrease (0.9–6.4 $\mathrm{Tg\,C\,yr^{-1}}$) in organic carbon burial in lake sediments across the entire northern boreal zone by the end of the 21st century [*Gudasz et al.*, 2010]. These estimates are based on an assumption that future organic carbon delivery to lake sediments will be similar to present-day conditions. Even with enhanced delivery, as might be expected with thawing permafrost, rising temperatures are noted to increase organic carbon mineralization, thereby lowering burial efficiency.

2.3. Altered Landscapes, Successional Trajectories, and Creation or Loss of Habitats

Changes in hydrological and cryospheric conditions (e.g., permafrost thaw and snow redistribution) collectively contribute to transformations of the landscape that lead to alterations in the structure and function of Arctic ecosystems [*Rowland et al.*, 2010; *Karlsson et al.*, 2011]. For example the presence of water in its different forms (liquid, solid, and gaseous state) has a mediating influence on several important ecosystem characteristics. Changes in permafrost conditions, type or timing of annual precipitation input, and evapotranspiration rates may have significant effects on the amount of available soil water, which in turn plays a significant role in determining the species distribution, plant community composition, primary productivity, and related successional patterns and nutrient transport and cycling [*Kane et al.*, 1992; *Hodkinson et al.*, 1999; *Chapin et al.*, 2006].

The combination of gradual, directional climate change coupled with multiple ecological feedback processes, many of which include and are propagated and mediated by water, may in turn cause surprising reorganizations of ecological structure and function and trigger ecosystem shifts or the development of novel ecosystems (Figure 3) [*Holling*, 1973; *Scheffer and Carpenter*, 2003; *Chapin et al.*, 2006; *Lindenmayer et al.*, 2010]. A number of such ecosystem shifts have been observed in the Arctic, including vegetation shifts and conversions between terrestrial and aquatic ecosystems [*Karlsson et al.*, 2011]. Below we discuss some of the prominent ecosystem shifts and habitat gains and losses observed in Arctic terrestrial and freshwater ecosystems that are directly or indirectly coupled to changes in hydrologic and/or related cryospheric regimes.

2.3.1. Coniferous to Deciduous Boreal Forest

Deciduous trees are slowly replacing coniferous-dominated boreal forest related to recent climate warming and intensification of the wildfire regime [*Johnstone et al.*, 2010a, 2010b]. Coniferous trees dominate the boreal forest under cold and moist conditions, which are often associated with a deep soil organic layer [*Johnstone et al.*, 2010a, 2010b]. Deciduous trees, by contrast, dominate under warm and dry conditions in nutrient-rich soils with a shallow organic layer. A warmer and drier climate may change the underlying soil conditions (temperature and moisture) to make vegetation and soils prone to more frequent and severe wild fire. Severe fires that consume the whole organic layer in the coniferous forest may alter the soil conditions to make them less favorable for recolonization by coniferous trees and more suitable for deciduous trees,

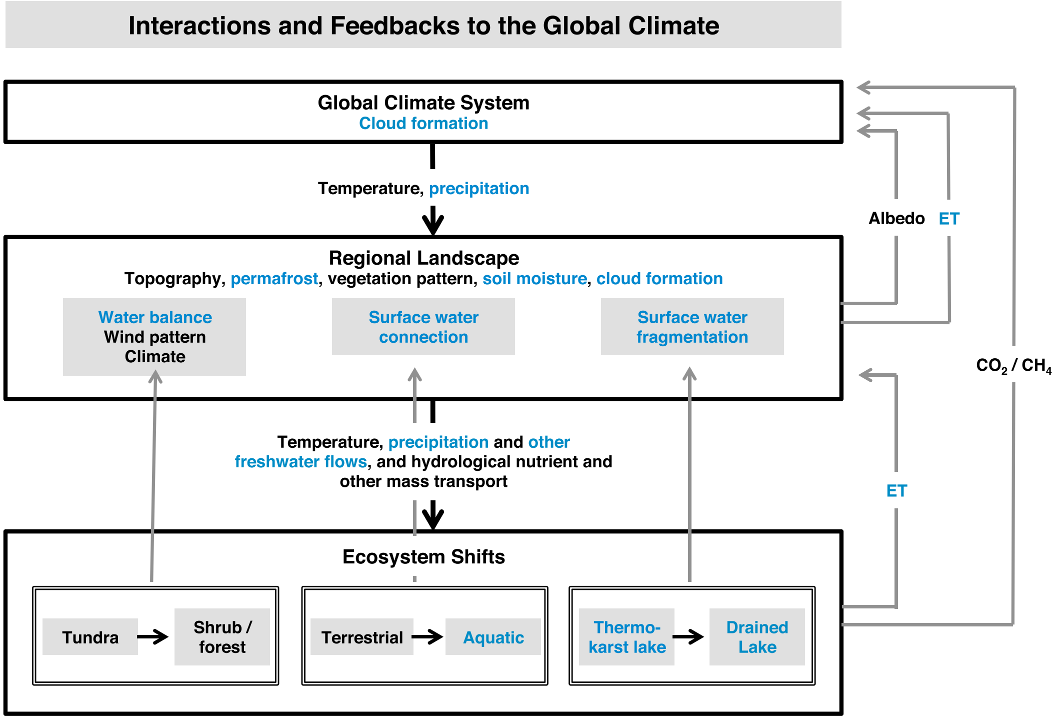

Figure 3. Interactions and feedbacks from three general types of shifts in Arctic terrestrial and freshwater ecosystems. Climate change drives changes in regional temperature and precipitation, and these exogenous changes interact with regional topography and landscape patterns of permafrost and plant communities and are mediated and propagated by hydrology (blue text indicating hydrologic variables) in pushing Arctic ecosystems toward directional ecosystem shifts (black arrows). Ecosystem shifts occur at the local landscape scale, but the consequences can feed back to regional and global scales (gray arrows), through, e.g., reshaping of hydrology (changes in evapotranspiration (ET), water balance, and surface water connection/fragmentation) and by altering albedo, and carbon (CO_2 and CH_4), energy fluxes. If these changes accumulate across large geographic areas, they can also affect the global climate [adapted from *Karlsson et al.*, 2011].

resulting in a shift in forest composition [*Johnstone et al.*, 2010a, 2010b; *Hollingsworth et al.*, 2013]. Moreover, as deciduous species are less flammable than conifer species, it is reasonable to believe that a potential expansion of deciduous species in boreal forests, either occurring naturally or through landscape management, could offset some of the impacts of climate change on the occurrence of boreal wildfires [*Terrier et al.*, 2013].

Although less severe (due to the lack of a thick soil organic layer, and thus fuel) than coniferous forests, wildfires tend to be more frequent in deciduous-dominated forests and this maintains conditions favorable for the regeneration of deciduous trees [*Johnstone et al.*, 2010a, 2010b]. A shift from coniferous to deciduous forest will have further implications on the hydrological system. Deciduous stands have higher evaporation and transpiration rates than coniferous stands, where most (nearly 90%) of the precipitation is returned to the atmosphere by transpiration resulting in water loss of the basin [*Baldocchi et al.*, 2000].

2.3.2. Tundra to Shrubland or Forest

Shrub expansion has been observed throughout the Arctic tundra during the past 50 years, slowly converting tundra ecosystems to shrubland or forest [*Tape et al.*, 2006; *Devi et al.*, 2008; *Kharuk et al.*, 2008; *Kammer et al.*, 2009; *Tommervik et al.*, 2009; *Forbes et al.*, 2010; *Myers-Smith et al.*, 2011; *Tape et al.*, 2012; *Frost et al.*, 2013; *Fraser et al.*, 2014]. The underlying drivers of shrub expansion are largely attributed to increasing air and soil temperature in combination with a lengthening in growing season [*Myers-Smith et al.*, 2015, and references therein]. However, many other factors related to local hydrological change influence shrub growth, e.g., precipitation, soil moisture, snowpack and snowmelt timing, permafrost disturbance, and erosion [*Myers-Smith et al.*, 2011; *Tape et al.*, 2012; *Frost et al.*, 2013; *Myers-Smith et al.*, 2015]. Previous studies have also shown that shrubs are preferentially expanding into riparian areas [*Naito and Cairns*, 2011; *Tape et al.*, 2012, 2015]. Increased grazing by herbivores may, by contrast, impede shrub expansion [*Post and Pedersen*, 2008;

Olofsson et al., 2009; *Tape et al.*, 2015]. The transition from tundra to shrubland or forest has implications for the hydrological cycle, as increases in shrub and tree cover, in turn, increase evapotranspiration and thereby loss of water (Figure 3) [*White et al.*, 2007; *Pearson et al.*, 2013; *Nauta et al.*, 2015].

2.3.3. Conversion Between Terrestrial and Aquatic Ecosystems Through a Changing Cryosphere

The presence and persistence of permafrost is a key physical factor influencing the existence of Arctic lakes and ponds, and the observed widespread lake changes are often linked to climate warming [*Smith et al.*, 2005, 2007]. An expansion in total lake area has been observed in continuous permafrost or in supraglacial environments [*Walter et al.*, 2006; *Smith et al.*, 2007; *Labrecque et al.*, 2009; *Marsh et al.*, 2009; *Leeson et al.*, 2015; *Paquette et al.*, 2015], while a decline has occurred in discontinuous and sporadic permafrost regions [*Yoshikawa and Hinzman*, 2003; *Riordan et al.*, 2006; *Jorgenson et al.*, 2006; *Sannel and Kuhry*, 2011; *Jones et al.*, 2011], suggesting that warming of permafrost initially causes thermokarst development and lake expansion, which is later followed by lake drainage as permafrost degradation continues. Thermokarst lakes and wetlands are developing in continuous permafrost environments where melting of ground ice and surface settlement are initiating ponding [*Labrecque et al.*, 2009; *Marsh et al.*, 2009].

Adding to the observed complexity, other studies have reported loss of lake area in ice-rich continuous permafrost [*Grosse et al.*, 2010; *Jones et al.*, 2011] and increases in lake area in discontinuous permafrost [*Payette et al.*, 2004; *Karlsson et al.*, 2012; *Watts et al.*, 2012], as well as relatively stable lake areas in regions that have experienced almost complete permafrost loss [*Bouchard et al.*, 2014]. The loss of Arctic deltaic lakes and ponds has also been attributed to a reduction in ice jam events in river floodplains [*Lesack and Marsh*, 2010], to the collapse of ice shelves and the associated loss of supraglacial and epishelf lakes [*Veillette et al.*, 2008], to increased net evaporation [*Smol and Douglas*, 2007; *Bouchard et al.*, 2013] or to thermokarst erosion and drainage [*van Huissteden et al.*, 2011], and to infilling resulting from aquatic plant growth [*Andresen and Lougheed*, 2015].

Such permafrost-related changes can convert terrestrial ecosystems (e.g., tree- and shrub-dominated forests) into aquatic ecosystems (wet sedge meadows, bogs, and thermokarst lakes), as thawing permafrost leads to continuous flooding of roots leading to collapse and death of trees [*Osterkamp et al.*, 2000; *Hinzman et al.*, 2005; *Karlsson et al.*, 2011]. The development of wetlands and thermokarst lakes feeds back to a warming climate by increasing methane emissions (Figure 3) [*McGuire et al.*, 2006; *Laurion et al.*, 2010]. Impacts of a shift from terrestrial to aquatic ecosystems include increase in surface water connectivity, as well as large habitat change and shifts in species composition, as water table depth and soil moisture change affect organic matter decomposition and nutrient availability (Figure 3).

In contrast, in regions where permafrost continues to thaw, thermokarst processes can also drain lakes and wetlands [*Yoshikawa and Hinzman*, 2003] and cause a transition from a surface water-dominated to groundwater-dominated hydrological system [*Karlsson et al.*, 2012]. Draining of lakes and wetlands causes conversion from aquatic to terrestrial ecosystems that can also result in climate feedbacks, as a drop in water table levels will influence the magnitude of CO_2 exchange and ecosystem productivity (Figure 3) [*McGuire et al.*, 2006]. The net effect of drier conditions associated with a declining water table on carbon exchange as a whole is, however, uncertain and will depend on the balance between increase in CO_2 efflux and decrease in methane efflux and increased carbon storage in new vegetation biomass [*McGuire et al.*, 2006]. Impacts of the shift from aquatic to terrestrial ecosystems include surface water fragmentation and decrease in surface water availability (Figure 3), which has a large impact on people, fish, and wildlife in the Arctic where access to liquid water is already restricted during a large part of the year [*White et al.*, 2007].

2.3.4. Changes in River/Lake Ice Regimes

Reductions in river ice jam flooding may have major positive benefits for communities and infrastructure located along the river margins but could also alter the ecology of deltaic riparian [*Lesack and Marsh*, 2007, 2010] and coastal marine [*Emmerton et al.*, 2008] ecosystems. The chemical composition, particulate organic carbon, and sediment loads of river water entering the marine environment during the spring period are projected to be affected with the reduction or loss of stamukhi lakes (freshwater impounded behind nearshore pressure ridges or grounded sea ice) and their distinct microbial assemblages, which play a key functional role in processing river inputs to the marine ecosystems [*Dumas et al.*, 2006; *Galand et al.*, 2008]. Associated ecological impacts of enhanced shoreline retrogressive slumping in thermokarst lakes in the western Canadian Arctic have also been shown to have significant implications for the geochemistry and aquatic food web structure and function of these systems [*Kokelj et al.*, 2009; *Mesquita et al.*, 2010; *Thompson et al.*, 2012; *Moquin et al.*, 2014].

Changes in near-coastal freshwater environments have also been documented for the case of epishelf lakes, such as on northern Ellesmere Island [*Veillette et al.*, 2008]. These ice-dependent freshwater lakes have become increasingly inundated with seawater as a result of the loss of integrity in their retaining ice dams [*Vincent et al.*, 2009]. As a result, the microbiologically rich ice shelf lakes are disappearing completely following their melting and collapse [*Mueller et al.*, 2008]. The timing and duration of lake ice cover also have a controlling influence on pelagic water column oxygen conditions and resulting habitat quality and quantity for fish and other aquatic biota [e.g., *Reist et al.*, 2006a, 2006b; *Vincent et al.*, 2008; *Laurion et al.*, 2010]. The occurrences of such events are forecasted to be reduced in a warmer climate with shortening ice duration, with potential cascading effects on lower trophic levels [*Balayla et al.*, 2010].

Altered river levels, combined with rising Arctic sea level and sea ice recession, have been proposed as the proximal drivers of biodiversity loss in Arctic deltaic river systems, primarily related to the loss of lakes with short and variable connection times plus low and variable river water renewal [*Lesack and Marsh*, 2010]. Deltas located at the terminus of most major Arctic rivers also act as biogeochemical processing regions for river water before its discharge to the sea [*Emmerton et al.*, 2008]. Hence, changes in the deltaic ice jam and related flooding regimes will affect deltaic and nearshore marine habitat quality and quantity.

Collectively, these studies highlight that significant complexities and regional uncertainties remain in predicting ecosystem and habitat creation and loss and associated cascading ecological impacts in relation to a changing Arctic freshwater system and related cryospheric regimes.

2.4. Altered Seasonality and Phenological Mismatches

Changes and mismatches in phenology between mutually dependent species have been observed in both terrestrial and freshwater ecosystems in the Arctic. There is increasing evidence that climatic change, often coupled with hydrological codrivers such as the timing and extent of snow or ice onset and melt, change in the frequency and intensity of rain on snow events, and earlier river and lake ice breakup, can have significant implications on time-sensitive ecological relationships. Examples include influences on the timing of green up, flowering, and senescence in tundra plants [*Oberbauer et al.*, 2013; *Gauthier et al.*, 2013; *Bjorkman et al.*, 2015]; the reproduction and migratory patterns of terrestrial and aquatic organisms; and predator-prey, plant-pollinator, and host-parasite interactions [*Woodward et al.*, 2010; *Donnelly et al.*, 2011; *Kerby and Post*, 2013a; *Xu et al.*, 2013; *Ims et al.*, 2013; *Wrona et al.*, 2013]. In turn, this can lead to changes in reproduction and survival, and hence to changes in populations of Arctic mammals (e.g., caribou and musk ox [*Post and Forchhammer*, 2008; *Miller-Rushing et al.*, 2010; *Clausen and Clausen*, 2013; *Ims et al.*, 2013; *Kerby and Post*, 2013b]) and birds (e.g., brent goose [*Clausen and Clausen*, 2013]; Baird's sandpiper [McKinnon et al., 2012]; greater snow goose [*Doiron et al.*, 2014]; and terrestrial and aquatic plants [*Daniëls et al.*, 2013]).

In freshwater ecosystems, increased water temperature and longer open-water periods are expected to shift seasonal phenology and to cause decreases in cold stenotherms (algae, benthic macroinvertebrates, and fish) and range alteration for cold-intolerant taxa [*Reist et al.*, 2006a, 2006b; *Culp et al.*, 2012]. Likely examples of potential mismatches would include early insect emergence that negatively affects fish feeding or that could expose larval insects in rivers to harmful spring flood disturbances. Moreover, altered seasonality may change important biotic interaction regimes (i.e., competition and predation), increase the geographic range of detrimental parasites and diseases [*Marcogliese*, 2001, 2008; *Hoberg and Kutz*, 2013], and ultimately lead to substantial changes in riverine and lentic food webs [*Wrona et al.*, 2013].

2.5. Gains or Losses of Species

Some of the consequences of a changing freshwater system of greatest local concern are those associated with the range expansion or contraction of plant, animal, and microbial species. In part, this is associated with the potential loss of species from northern ecological communities, but this is also associated with the arrival of new species from the south, either through gradual range expansions or long-distance dispersal of invasive species [*Callaghan et al.*, 2004c; *Culp et al.*, 2012; *Christiansen et al.*, 2013; *Ims et al.*, 2013; *Wrona et al.*, 2013; *Miller and Ruiz*, 2014; *Wisz et al.*, 2015].

Gains or losses of species and shifts in community composition in both terrestrial and freshwater ecosystems can be the result of a variety of mechanisms that may operate individually or in concert. These include the creation of new habitat space (see section 2.3), a modification of the existing habitat or food web that is favorable to new species, and enhancement of the ability of invasive species to invade new habitats/ecosystems (e.g., increased interconnectivity of Arctic lake-river complexes via permafrost thaw [*Wrona et al*., 2013]). In addition, changes in thermal regimes from climate warming may lead to change in community composition, favoring more warm-adapted species [*Christiansen et al*., 2013; *Elmendorf et al*., 2015]. Local extinctions may be caused by the crossing of physiological or ecological thresholds (e.g., Arctic fox [*Gallant et al*., 2012; *Hof et al*., 2012]) or by competitive exclusion caused by newly arrived species (e.g., fish species [*Reist et al*., 2006a, 2006b; *Sharma et al*., 2007]). Patterns of aquatic species richness and diversity are projected to change with alterations to ice, open-water duration, and flow regimes, in turn allowing the arrival of southern species such as, for example, bloom-forming cyanobacteria [*Vincent and Quesada*, 2012] and fish [*Reist et al*., 2006a, 2006b]. The diverse, highly stratified communities of single-celled Archaea in high-Arctic lakes are likely to be disrupted by future changes in the duration of ice cover [*Pouliot et al*., 2009], although increased open water is also projected to promote the development of new trophic levels and the successful colonization of new aquatic species assemblages [e.g., *Vincent et al*., 2009].

Species range expansions can also arise from shifts in dispersal pathways and intensities (e.g., bird migration pathways [*Gillespie et al*., 2012], which can occur in concert with, for example, climate warming). Highly invasive warm-water species such as the waterweed *Elodea canadensis*, the ruffe *Gymnocephalus cernuus*, and the common carp *Cyprinus carpio* all have the potential for enhanced northern range expansion related to climate warming and increased interconnectivity of aquatic environments from an intensified hydrological cycle [*Madsen and Brix*, 1997; *Badiou and Goldsborough*, 2006; *Rahel and Olden*, 2008; *Heikkinen et al*., 2009]. Host-parasite-disease distributions and related trophic interactions will also be altered with fish [*Reist et al*., 2006a, 2006b] and terrestrial species (e.g., caribou and musk ox [*Kutz et al*., 2013]) expanding their current range into northern habitats and bringing associated parasite fauna and diseases [*Marcogliese*, 2001, 2008; *Hoberg et al*., 2003; *Hoberg and Kutz*, 2013].

These effects may be further amplified by secondary environmental drivers such as disturbance in the system (e.g., permafrost [*Thienpont et al*., 2013], fire [*Mack et al*., 2011], transport infrastructure [*Smith and Stephenson*, 2013], and resource development [*Forbes et al*., 2001; *Kumpula et al*., 2011]).

3. Implications for Ecosystem Services

A modified and intensified Arctic freshwater system, coupled with other climate-related drivers of change (e.g., temperature, evaporation, evapotranspiration, and nutrient availability), can individually and cumulatively have profound implications for the status, trends, and plausible futures of the ecosystem services provided by terrestrial and freshwater systems.

Complex interrelationships exist among dominant environmental and anthropogenic drivers and their potential effects on terrestrial and freshwater systems and their related services [*Hooper et al*., 2005; *Wrona et al*., 2013]. Combinations of drivers can interact across a range of spatial, temporal, and organizational scales, resulting most often in synergistic or cumulative effects [*Nelson et al*., 2006; *White et al*., 2007; *Schindler and Lee*, 2010]. Arctic terrestrial and freshwater ecosystems contain a multitude of habitats of varying ecological complexity and support a diversity of permanent and transitory organisms adapted to living in seasonally variable and extreme environments. These habitats and species provide important ecological and economic services to northern peoples through subsistence foods (fish, waterfowl, and mammals), seasonally important transportation corridors (e.g., ice roads), and ecologically and culturally important habitats for resident and migratory species [*Prowse et al*., 2011; *Wrona et al*., 2013]. Given that Arctic terrestrial and freshwater ecosystems provide a range of ecological goods and services to humans at local, regional, and global scales, understanding the complex interactions among hydrological factors and their combined, cumulative effects with other environmental and anthropogenic drivers on ecosystem structural and functional properties remains a key scientific and management challenge [*ACIA*, 2005; *White et al*., 2007; *SWIPA*, 2011; *ABA*, 2013].

Changes in biological productivity resulting from an altered freshwater cycle have consequences for traditionally harvested species such as caribou/reindeer, waterfowl, and Arctic char and on related ecotourism activities [*ACIA*, 2005; *Reist et al*., 2006a, 2006b; *Christiansen et al*., 2013; *Huntington et al*., 2013; *Prowse* *et al*., 2011]. Both the greening and browning of Arctic freshwaters will result in increased biological production in the water column, and less in the benthos (see section 2.2), thereby affecting trophic relationships for valued fish species such as Arctic char [*Reist et al*., 2006a, 2006b; *Christiansen et al*., 2013]. Arctic freshwater and diadromous fishes have historically been, and continue to be, of significant importance to humans inside the Arctic region, particularly food/subsistence fisheries by indigenous peoples [*Christiansen et al*., 2013; *Huntington et al*., 2013]. Excessive nutrient input may also lead to the development of toxic cyanobacterial blooms that affect drinking water quality as well as food web relationships [*Jeppesen et al*., 2010, 2013; see also *Instanes et al*., 2016].

Hydrologically induced changes in Arctic terrestrial and freshwater geochemical cycling could have important implications related to the release, distribution, and fate of chemical elements and compounds such as nutrients, heavy metals, and volatile organic compounds [*Macdonald et al*., 2005; *MacMillan et al*., 2015]. Increased inputs of nutrients, through a thicker active layer and enhanced subsurface and surface water flows, could lead to the eutrophication of aquatic systems (both freshwater and nearshore estuarine marine), thereby altering local and regional species richness and related biodiversity, food web structure and interactions, and biogeochemical cycling [*Carmack et al*., 2016; *Wrona et al*., 2013; *Jeppesen et al*., 2010]. Hydrological alteration in the release, transport, and fate of contaminants also has significant potential implications for the bioaccumulation of persistent organic pollutants or metals in wildlife and fish species [*Wrona et al*., 2006b; *Macdonald et al*., 2005; *AMAP*, 2003]. Enhanced release and transport of dimethyl sulfide, which is the most abundant biological sulfur compound emitted to the atmosphere, have implications for the creation of new aerosols which influence cloud formation [*Vihma et al*., 2016].

Enhanced Arctic shrubification resulting from changes in both climate and hydrologic drivers can potentially reduce the availability of forage for wildlife species including for example lichen habitats which caribou prefer and, by contrast, increase habitat suitable for moose [*Tape et al*., 2015]. Vegetation changes also affect subsistence hunting opportunities because the increase in shrub and tree growth impedes transportation across tundra landscapes [*Stern and Gaden*, 2015]. Conversely, it also has the potential to increase timber production. Loss or change of aquatic ecosystems can alter the magnitude and temporal pattern of streamflow and impact on water quality and availability for both rural and urban peoples as well as for industry [*White et al*., 2007; *Instanes et al*., 2016].

The gains or losses of terrestrial and/or aquatic species (including the introduction of invasive species) can have a profound effect on the structure and function of impacted ecosystems. For example, the arrival of dam-forming beavers, nitrogen-fixing alder [*Tape et al*., 2006], or mat-forming cyanobacteria may alter flow regimes, evaporation and water balance, and substrate stability. This may impact on conservation values and suitability of terrestrial and aquatic ecosystems for cultural use, including subsistence hunting, or lead to substantial effects on drinking water safety (e.g., enhanced occurrence of toxic cyanobacteria, water pathogens, etc.) [*Schindler and Lee*, 2010; *White et al*., 2007].

4. Knowledge Gaps and Future Directions

Based on historical and present observational data and forecast changes in the global climate system, Arctic terrestrial and freshwater ecosystems are increasingly affected by environmental drivers related to alterations in the terrestrial hydrological and related climatic regimes. Developing an improved predictive understanding of the responses and future trajectories of ecosystems to concomitant changes in hydrological processes (e.g., enhanced frequency and duration of extreme low and high flows and changes in the duration of snow and ice cover) will be paramount to the development and implementation of possible adaptation measures. However, as emphasized in *Bring et al*. [2016], *Lique et al*. [2016], *Prowse et al*. [2015b], and *Vihma et al*. [2016], significant uncertainties remain in having an adequate process-based understanding of the environmental factors affecting the rates and magnitudes of hydrologic responses at relevant spatial and temporal scales to assess and predict changes in ecosystem responses. Such information will be critical in informing new and adaptive environmental conservation and management approaches and practices at local, regional, and circumpolar scales.

Table 1 summarizes the key questions and knowledge gaps that have been identified through this assessment, with a specific focus on Arctic terrestrial and freshwater ecosystems. In addition, we propose the following focal areas for future coordinated cross-disciplinary research and monitoring that should be

Table 1. Key Ecosystem Attributes and Processes That Are Observed or Projected to Be Affected by a Changing Arctic Freshwater System and Associated Key Questions and Knowledge Gaps That Need to Be Addressed Through Enhanced, Interdisciplinary Research and Monitoring

Ecosystem Attributes/Processes	Questions and Knowledge Gaps
Productivity changes	What are the rates and relative importance of greening and browning in terrestrial and freshwater ecosystems under an intensified Arctic freshwater system? What is the relative importance of under-ice/snow productivity in terrestrial and freshwater ecosystems under changing hydrologic and cryospheric conditions?
Altered biophysical properties, biogeochemical cycles, and chemical transport	Which Arctic regions are most vulnerable to ecosystem shifts or alterations in ecosystem properties such as nutrient cycling and energy and material flow in the future? Will alterations in ecosystem biophysical and biogeochemical properties have a cascading influence on other systems and areas, and how will these effects interact on contrasting spatial and temporal scales? How will changes in sunlight exposure, along with shifts in hydrologic properties such as residence time, affect the photochemical-biogeochemical processing of dissolved organic carbon in freshwater systems? How does increased terrestrial and freshwater productivity influence biogeochemical exports to the ocean? How does an intensified hydrological cycle influence net emissions of greenhouse gases?
Altered landscapes, successional trajectories, and creation of new habitats	What are the novel successional trajectories/ecosystems that will develop in Arctic ecosystems? What ecosystem types will be lost and how will one know when this loss occurs? Can we identify ecological vulnerability or risk of state change?
Altered seasonality	How will altered seasonality influence the productivity of Arctic terrestrial and freshwater ecosystems? What is the extent and magnitude of phenological mismatches and their effect on the structure and function of Arctic food webs? What are the cascading ecological consequences of altered seasonality in terms of terrestrial-freshwater-marine ecosystem coupling and related processes? Will phenological mismatch restructure Arctic food webs and lead to cascading ecological processes?
Species gains and losses	How will changes in community composition through gains and/or losses of species influence ecosystem function; is there “functional resilience”? How quickly will range expansions or invasive species restructure Arctic ecosystems? What terrestrial and freshwater ecosystems are the most vulnerable to species losses or gains?

undertaken to advance understanding of the ecological effects from an altered and intensified Arctic hydrological system: (1) forecasting of rates and relative importance of greening and browning in terrestrial and freshwater systems, including an improved process-based understanding of interecosystem interactions that involve terrestrial landscape-freshwater-nearshore marine coupling; (2) prediction of how an altered and intensified hydrological cycle affects terrestrial and freshwater productivity and influences biogeochemical processes such as net emissions of greenhouse gases and geochemical exports to the ocean; (3) identification of specific Arctic regions that may be most vulnerable to ecosystem shifts in the future (e.g., shrubification, species gains and losses, enhanced landscape disturbance/alterations such as thermokarst development, and slumping) and determination of whether tipping points exist that lead to irreversible ecosystem state changes; (4) projection of how altered hydrological and climatic seasonality will influence the structure and function of Arctic ecosystems and determination of whether phenological mismatches will result in restructuring of Arctic food webs and corresponding cascades to ecological processes; (5) improved process-based understanding and prediction of hydrological and cryospheric change at relevant spatial and temporal scales to assess corresponding changes in geochemical, biological, and ecosystem-level attributes and properties.

To improve process-based and predictive understanding of how Arctic terrestrial and freshwater ecosystems will respond to terrestrial hydrological and climate-related change requires new approaches that identify and quantify the key interconnections (e.g., geochemical fluxes and material and energy flow) between the various systems (i.e., the coupling of atmosphere, landscape, freshwater, and marine systems and processes). There is a need for systematic and integrated observational and research networks in the Arctic that explicitly address the mismatch of scales in environmental attributes and processes (both temporal and spatial) and identify the state variables and process that must be measured and coupled across ecosystems [*Prowse et al.*, 2015b].

A pragmatic approach will be to expand the use of the “catchment scale” as an integrating hydroecological unit of study that couples terrestrial, freshwater, and nearshore ocean environments and processes in more geographically defined fluvial systems [e.g., *Ferrier and Jenkins*, 2010; *Schindler and Lee*, 2010

Skeffington et al., 2010; *Wrona et al*., 2013]. Such an approach builds on the works of *Williamson et al*. [2008, 2009] and *Schindler* [2009] who identified streams, lakes, and reservoirs as a distributed network of freshwater ecosystems that provide both historical and contemporary information of how terrestrial and aquatic ecosystems respond to climate change. A catchment-based approach explicitly links the hydrological cycle with landscape and land use change and recognizes the interconnectivity of terrestrial ecosystem responses and processes with both surface water systems (wetlands, lakes, rivers, deltas, and coasts) and subsurface water (groundwater) processes [*Ferrier and Jenkins*, 2010; *Verdonschot et al*., 2012; *Karlsson et al*., 2012].

Integrated, cross-disciplinary catchment-based studies and monitoring will allow, for example, for the development of improved process-based understanding of how changes in the types (i.e., snow versus rain), magnitudes, duration, and frequency of precipitation regimes at the catchment and subcatchment scales affect cryospheric and discharge regimes, related geochemical and sediment fluxes, and corresponding ecosystem structure and function. Further catchment subclassification (e.g., habitat delineation using soil moisture gradients in the terrestrial landscape; erosional versus deposition reaches in riverine systems; and shallow, well-mixed versus thermally stratified lakes) will allow for finer-scaled investigations of the causal mechanisms of observed and projected hydroecological changes.

It is increasingly recognized that interdisciplinary approaches to monitoring, research, and modeling will be crucial for the understanding and prediction of hydroclimatic landscape-land use ecosystem interactions and responses of Arctic ecosystems to the rapidly changing climate and terrestrial hydrological conditions [e.g., *Ferrier and Jenkins*, 2010; *Karlsson et al*., 2011; *Wrona et al*., 2013; *Larsen et al*., 2014; *Prowse et al*., 2015b]. Further coordinated efforts are required to develop and validate integrated, catchment-based models that couple climate projections and scenarios to measureable hydrologically related (e.g., soil moisture, water flow, snow, and ice quantity and quality) and ecological attributes (e.g., water quality, distribution and abundance of organisms, productivity, and carbon and nutrient fluxes) at relevant scales [*Skeffington et al*., 2010; *Verdonschot et al*., 2010; *White et al*., 2007; *Lique et al*., 2016]. Significant insights will be gained where the terrestrial-freshwater continuum of fluxes and processes are investigated across a full spatial range of hydroecological units (e.g., from headwater wetlands/ponds to river/lakes complexes to the nearshore ocean environment). This will be particularly true in geographic areas of the Arctic that are currently undergoing or are projected to have significant changes in the hydroclimatic and related cryospheric regimes, as highlighted by *Bring et al*. [2016], *Lique et al*. [2016], *Prowse et al*. [2015b], and *Vihma et al*. [2016]. Using a hierarchical approach will provide increasingly relevant information to inform decision making related to socioeconomic factors and implications and inform terrestrial and freshwater ecosystem-adaptive management options under a changing Arctic freshwater system.

Acknowledgments
The Arctic Freshwater Synthesis has been sponsored by the World Climate Research Programme's Climate and the Cryosphere project (WCRP-CliC), the International Arctic Science Committee (IASC), and the Arctic Monitoring and Assessment Programme (AMAP). Additional support has been provided by the Norwegian Ministries of Environment and of Foreign Affairs, the Swedish Secretariat for Environmental Earth System Sciences (SSEESS), the Swedish Polar Research Secretariat, Environment Canada and the University of Victoria, B.C., Canada, and the Swedish Environmental Protection Agency. We gratefully acknowledge the project coordination and meeting support of Jenny Baeseman and Gwenaelle Hamon at the CliC International Project Office. All data referred to in the text and figures for this paper are properly cited and referred to in the reference list. Data may be obtained by contacting the corresponding author.

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