Climate-Mediated Changes to Linked Terrestrial and Marine Ecosystems across the Northeast Pacific Coastal Temperate Rainforest Margin

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Coastal margins are important areas of materials flux that link terrestrial and marine ecosystems. Consequently, climate-mediated changes to coastal terrestrial ecosystems and hydrologic regimes have high potential to influence nearshore ocean chemistry and food web dynamics. Research from tightly coupled, high-flux coastal ecosystems can advance understanding of terrestrial–marine links and climate sensitivities more generally. In the present article, we use the northeast Pacific coastal temperate rainforest as a model system to evaluate such links. We focus on key above- and belowground production and hydrological transport processes that control the land-to-ocean flow of materials and their influence on nearshore marine ecosystems. We evaluate how these connections may be altered by global climate change and we identify knowledge gaps in our understanding of the source, transport, and fate of terrestrial materials along this coastal margin. Finally, we propose five priority research themes in this region that are relevant for understanding coastal ecosystem links more broadly.

Keywords: temperate rainforest, coastal margin, climate change, carbon, terrestrial aquatic links

Coastal margins are highly active zones at the interface between land and ocean, encompassing tightly linked, dynamic, and productive ecosystems. These interconnected systems have received increasing scientific and public attention in recent years because of the recognition that approximately 40% of the world's human population lives within 100 kilometers (km) of the ocean, and climate change threatens the resilience of these complex social–ecological systems (IPCC 2014). Material fluxes from coastal watersheds subsidize estuarine processes and ocean productivity; however, climate-mediated changes to terrestrial ecosystems and hydrologic regimes are influencing elemental and organic matter transport to marine ecosystems and therefore altering nearshore ocean chemistry and food web dynamics (Ward et al. 2020). Regions with high hydrologic throughput that are experiencing accelerated rates of climatic change are especially vulnerable to such shifts and may have a disproportionate downstream influence (O'Neel et al. 2015). Tight coupling across ecosystem boundaries in coastal watersheds, combined with the climate sensitivity of key processes that influence materials flux (e.g., plant production, soil organic matter decomposition), may lead to unforeseen threshold responses and regime shifts in ecosystem functioning (Groffman et al. 2006).

Coastal temperate rainforests (CTRs) epitomize how connections between terrestrial, freshwater, and nearshore marine ecosystems are being altered by temperature increases, precipitation changes, and the loss of glacial mass. Mountainous coastlines dominated by fjords and island archipelagos often characterize CTR landscapes and this topographic network funnels large volumes of freshwater to nearshore systems because of the combination of steep terrain, high ocean-derived precipitation, and cumulative runoff from many small watersheds. With this hydrologic outflow comes abundant terrestrial material, including organic carbon (OC) and micronutrients, originating from carbon (C)-rich wetlands and dense forests and glacial weathering of underlying bedrock (Hood and Scott 2008,

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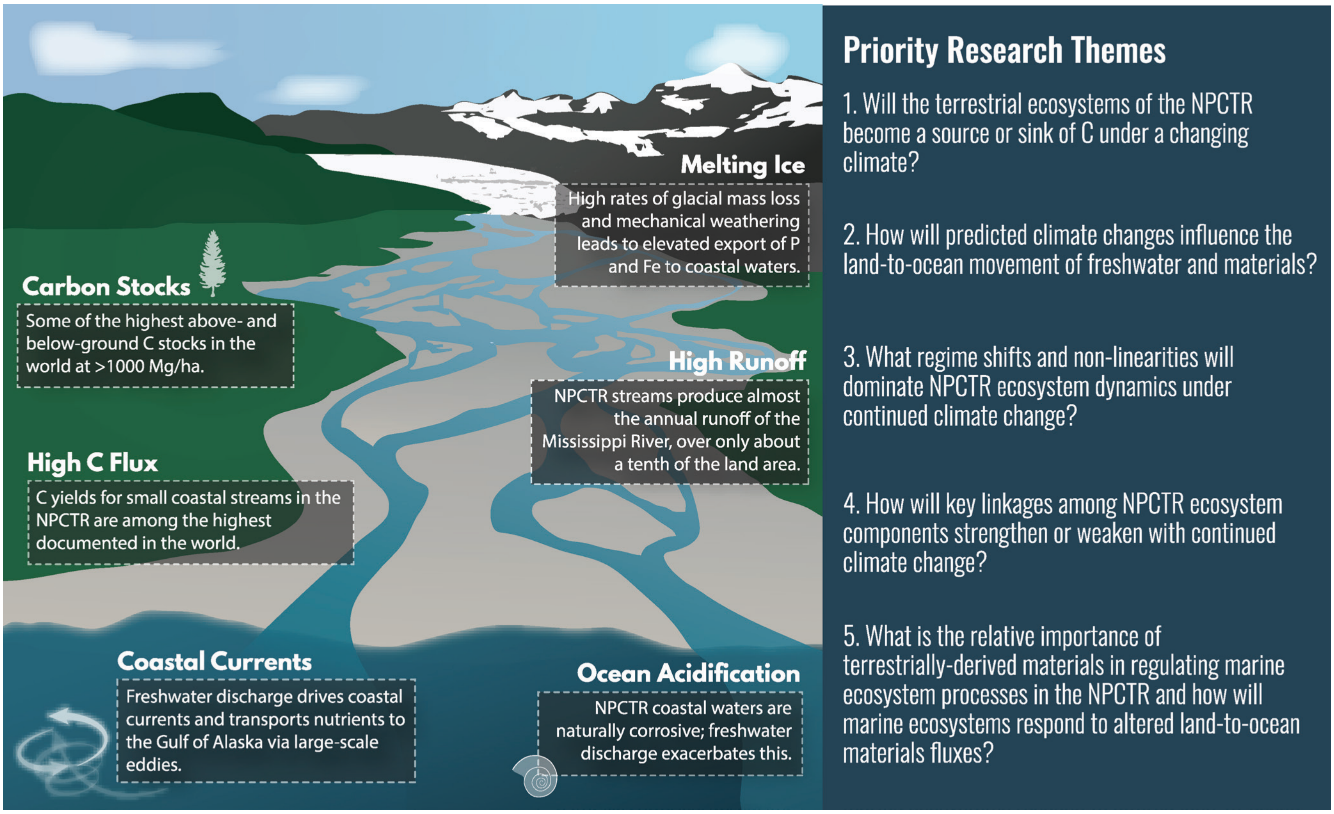


Carbon Stocks

Some of the highest above- and below-ground C stocks in the world at >1000 Mg/ha.

High C Flux

C yields for small coastal streams in the NPCTR are among the highest documented in the world.

Melting Ice

High rates of glacial mass loss and mechanical weathering leads to elevated export of P and Fe to coastal waters.

High Runoff

NPCTR streams produce almost the annual runoff of the Mississippi River, over only about a tenth of the land area.

Coastal Currents

Freshwater discharge drives coastal currents and transports nutrients to the Gulf of Alaska via large-scale eddies.

Ocean Acidification

NPCTR coastal waters are naturally corrosive; freshwater discharge exacerbates this.

Priority Research Themes

1. Will the terrestrial ecosystems of the NPCTR become a source or sink of C under a changing climate?
2. How will predicted climate changes influence the land-to-ocean movement of freshwater and materials?
3. What regime shifts and non-linearities will dominate NPCTR ecosystem dynamics under continued climate change?
4. How will key linkages among NPCTR ecosystem components strengthen or weaken with continued climate change?
5. What is the relative importance of terrestrially-derived materials in regulating marine ecosystem processes in the NPCTR and how will marine ecosystems respond to altered land-to-ocean materials fluxes?

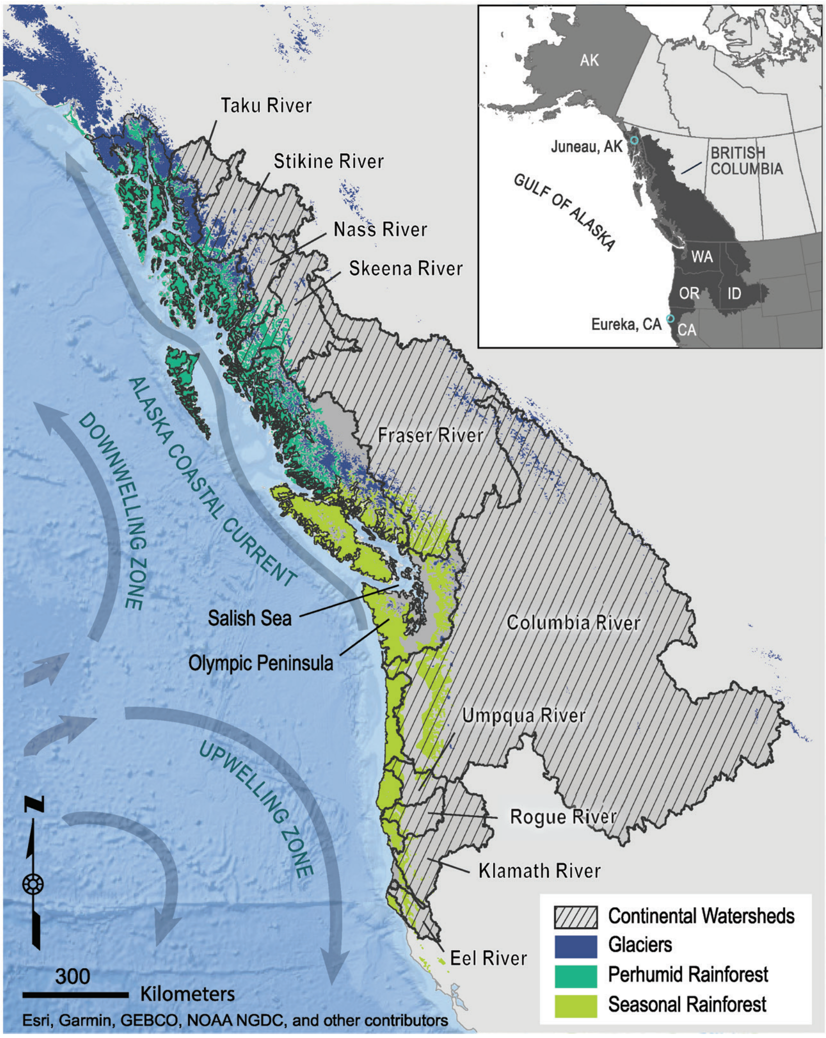
Figure 1. Key ecosystem characteristics of the northeast Pacific coastal temperate rainforest and priority research themes within the context of climate change.

D'Amore et al. 2015a, Edwards et al. 2020). Given the large OC stocks in CTR ecosystems and considerable hydrologically mediated material export to the ocean, climatic shifts are likely to have clear impacts on coastal materials processing with implications for global C and nutrient cycling (figure 1; Cloern et al. 2016).

Despite substantial research on some ecosystem components of CTRs, there has been relatively little holistic research on the ecosystem processes occurring across their coastal margins and any consequent impacts of climate change. Such high-flux ecosystems are potentially valuable for advancing broader understanding and predictive modeling of terrestrial–marine links and thresholds (Ward et al. 2020). For example, changes in watershed hydrology associated with climate-driven snow-to-rain transitions will shift the timing and magnitude of biogeochemical fluxes to coastal ecosystems and subsequent incorporation of terrigenous materials into marine food webs. In the present article, we use the northeast Pacific coastal temperate rainforest (NPCTR) as a model system to elucidate the key above- and belowground production and hydrological transport processes that control the land-to-ocean flow of materials and their influence on nearshore marine ecosystems, and evaluate how they may be altered by global climate change as expressed at regional scales. We also identify knowledge gaps in our understanding of the source, transport, and fate of terrestrial materials along this coastal margin and propose priority research themes in this region that are relevant for the understanding of coastal ecosystem links more broadly.

Ecoregion description

The NPCTR (figure 2) stretches more than 2000 km from south-central Alaska, in the United States, through British Columbia (BC), Canada, and down the coast to northern California, in the United States. The NPCTR is divided into four forested subregions, from north to south: subpolar (10,137 square kilometers [km^2]), perhumid (95,515 km^2), seasonal (116,714 km^2), and warm or coast redwood (8391 km^2; Kellogg 1995). This article centers exclusively on the largest subregions—the northern, perhumid, and southern, seasonal—which extend from just south of the Alsek River watershed in southeast Alaska to the Eel River watershed in California. These subregions represent the vast majority (92%) of the biome area, have broadly similar plant communities, and fall between the climate extremes of the snowy and cold subpolar forest in the north and the coastal fog-dominated redwood zone in the south. Hereafter, *NPCTR* will refer to these two subregions. Within the NPCTR, large and long-lived conifers, abundant peatland ecosystems, and deep soils store some of the highest amounts of C globally (combined above- and belowground, more than 1000 megagrams [Mg] per hectare [ha]; Smithwick et al. 2002, McNicol et al. 2019,



NORTH

- Wetter, cooler climate
- More snow and ice, ice-age glaciation
- Little to no wildfire
- Coastal landforms are fjords and islands with steep mountainous topography
- Downwelling oceanic regime
- Thousands of small, steep watersheds delivering most freshwater discharge
- Large proportion of wetlands with high below-ground C stocks
- Young, poorly drained soils

SOUTH

- Warmer, drier climate
- Less snow and ice, no ice-age glaciation
- Long fire intervals with increasing wildfire frequency and severity to the south
- Coastline becomes less incised south of the Salish Sea, and landforms include riparian valleys and mountains
- Upwelling oceanic regime
- Fewer coastal watersheds, higher influence of large continental rivers
- Higher above-ground C stocks in upland forests
- Well-developed, well-drained soils

Figure 2. Map of the northeast Pacific coastal temperate rainforest (NPCTR) drainage basin (dark gray, inset) and perhumid and seasonal rainforest subregions. The ten largest watersheds are delineated with hash marks; these all have substantial portions of their basins outside of the NPCTR. The remainder of the drainage area is characterized by extensive rainforest cover and a large number of smaller watersheds (Gonzalez Arriola et al. 2018). Current ecosystem heterogeneity from north (perhumid rainforest) to south (seasonal rainforest) is described. Bathymetry is from Esri (2020). Source: Adapted from Kellogg (1995).

Kauffman et al. 2020). The landscape has been largely shaped by several episodes of glaciation, combined with uplift and erosional processes, leading to a complex pattern of islands, incised coastal mountain ranges, fjordlands, wide glacial valleys, and lowlands. The presence of glacial ice and permanent snow is a defining characteristic of many NPCTR watersheds, however the region is experiencing some of the highest rates of glacial mass loss worldwide (Larsen et al. 2015).

Climatologically, the NPCTR is characterized by cool summers and relatively high precipitation (figure 3). Mean annual air temperature at sea level increases roughly 6 degrees Celsius (°C) from north to south, averaging 5.6°C at the northern end in Juneau, Alaska and 11.6°C at the southern end of the region in Eureka, California. Regional trends in precipitation are dominated by strong orographic effects that produce some of the highest annual rain- and snowfall in North America (in places more than 5000 millimeters annually). The vast amounts of precipitation that fall as rain and snow in the NPCTR, combined with steep topography and generally low evapotranspiration rates, translate to extremely high specific discharge rates and an overall massive volume of runoff into the North Pacific Ocean.

In the present article,we focus on the many small coastal watersheds of the NPCTR and exclude the 10 larger, well-studied rivers (e.g., Columbia, Fraser, Skeena) that originate east of the coastal mountain range and display hydrologic regimes typical of interior ecosystems and climates (figure 2). These coastal margin watersheds have marine,

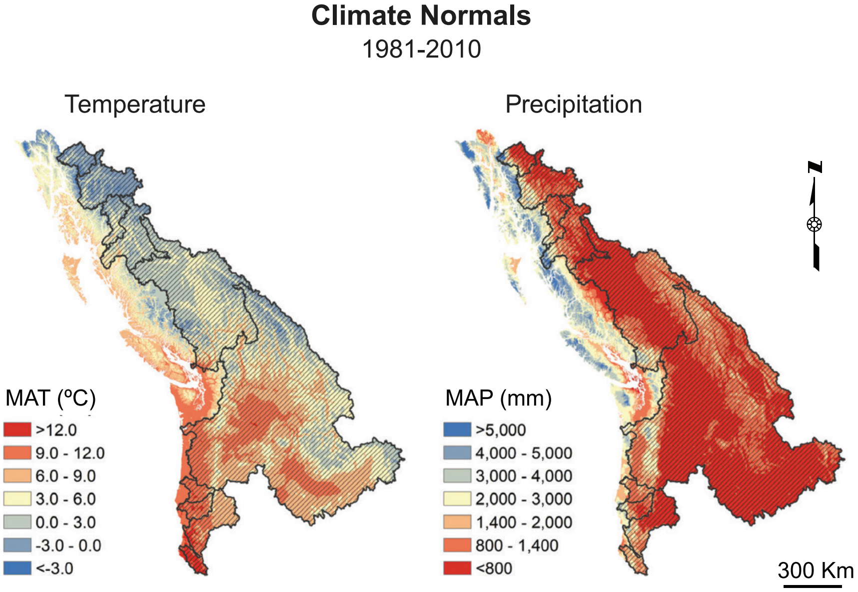


Figure 3. Regional climate normals (1981–2010) The outlines of the ten largest watersheds are shown with hash marks (Gonzalez Arriola et al. 2018). Source: The data are from Hamann et al. 2015, Wang et al. 2016). Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature.

west coast climate regimes and are much smaller (mean watershed size of 212 km^2 among delineated watersheds more than 20 km^2 versus 112,500 km^2; Gonzalez Arriola et al. 2018) and vastly more numerous ($n > 1000$) than the major rivers. Several studies modeling freshwater flux across the NPCTR suggest that these smaller watersheds contribute a disproportionately high volume of the freshwater flux to the ocean (e.g., Morrison et al. 2012, Hill et al. 2015). For example, in the area between (and including) the Columbia and Stikine rivers, the five biggest watersheds produce 57% of the regional annual discharge (568 cubic kilometers [km^3]); the remaining smaller coastal watersheds produce 43% of the discharge (429 km^3) while draining only 15% of the area (Morrison et al. 2012). By comparison, the magnitude of runoff from these thousands of small NPCTR streams approximates the annual runoff of the Mississippi River, although collectively these spatially distributed streams drain only about a tenth of its land area.

The flow of water across the NPCTR coastal margin facilitates large fluxes of nutrients and riverine OC, mainly as dissolved organic carbon (DOC). As a result, this region exhibits some of the highest documented yields of DOC for small coastal streams globally (D'Amore et al. 2015a, Oliver et al. 2017). Nitrogen (N) yields from NPCTR watersheds with high alder (*Alnus* spp.) coverage can be many times higher than from other forested ecosystems (Compton et al. 2003). Phosphorus (P) and iron (Fe) derived from mechanical weathering of bedrock by glaciers are also exported from NPCTR streams to the coastal ocean (Hood and Scott 2008, Schroth et al. 2011). Collectively, these terrestrially derived materials influence marine biogeochemistry and food webs (Wetz et al. 2006, Fellman et al. 2010, Arimitsu et al. 2018).

Freshwater flows combine with winds and tides to drive fjord and estuary circulation, front formation, and seasonal stratification. These local hydrodynamic processes influence nutrient dynamics, sediment loading, and light availability in the nearshore, which, in turn, affect primary productivity, plankton composition and biomass, and the diversity and productivity of higher trophic levels (Etherington et al. 2007, Arimitsu et al. 2016). The large volume of freshwater outflow from the NPCTR supports a contiguous coastal boundary current, the Riverine Coastal Domain (Carmack et al. 2015), that moves northward from the Columbia River and around the Gulf of Alaska (GOA; figure 2). Even farther offshore, freshwater and its associated terrestrially derived material are transported hundreds of kilometers westward over the continental shelf and into the GOA by large anticyclonic eddies (Ladd et al. 2009).

Notwithstanding widely shared ecosystem attributes across 20 degrees of latitude, the NPCTR spans broad gradients of glacierization, coastal hydrodynamics, and disturbance regimes (figure 2). The northern majority of the region—Alaska to the northeastern Olympic Peninsula—was glaciated during the Last Glacial Maximum and therefore exhibits a characteristic fjord landscape with thousands of small, steep coastal watersheds. The unglaciated portion from the western Olympic Peninsula south to California has a much different coastal physiography, with broader coastal floodplains, shallow bays, and fewer coastal watersheds. Generally, NPCTR coastal waters are divided into downwelling and upwelling domains, north and south of Queen Charlotte Sound, respectively. The downwelling domain receives marine nutrients by onshore transport of surface nutrients and late winter upward mixing of continental shelf waters, experiencing greater retention of freshwater and terrestrial material outflows in the coastal zone, whereas the upwelling domain receives large annual inputs of marine-derived nutrients from the deep ocean (Ware and McFarlane 1989). On land, very long fire return intervals characterize the northern NPCTR (Gavin et al. 2003), and there is less anthropogenic landscape modification compared with the southern NPCTR. In contrast, the southern NPCTR has a more pronounced fire regime (Gavin et al. 2013) and a history of extensive logging, agricultural conversion, and urbanization (Omernik and Gallant 1986). There is a similar gradient in anthropogenic impacts on freshwater and marine ecosystems from north to south, with dam infrastructure, declines in anadromous fisheries, and higher nutrient loads increasing as one moves from north to south.

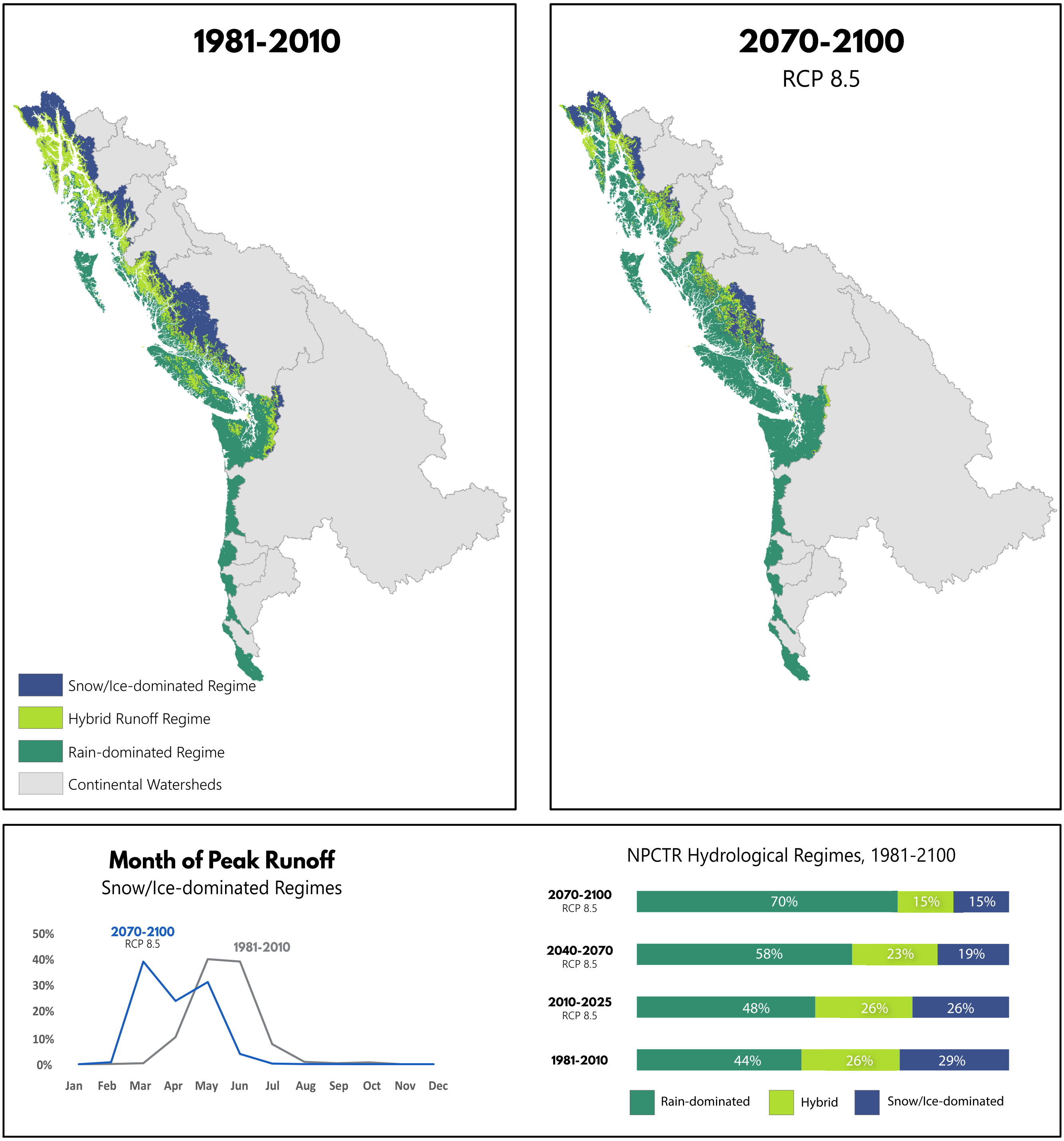


Figure 4. Gridded primary hydrologic regime (snow dominated, hybrid, rain dominated) types from 1981 to 2010 and projected shifts in distributions and timing of peak runoff under RCP 8.5. The figure was produced using the Distributed Climate Water Balance Model (Moore et al. 2012), using a single parameter set from Edwards and colleagues (2020), and run at a 400 meter pixel interval driven by ClimateNA normals and projections through 2080 (Wang et al. 2016). A total of 40 hydrographs representing snow dominated (15), hybrid (15), and rain dominated (10) from 1981 to 2010 were selected as a training data set, and then each 400 meter pixel across the domain was classified using a k nearest neighbor algorithm. To validate hydrograph typing, 200 KNN classifications from the 1981–2010 data set were randomly selected and manually classified, resulting in 98% agreement.

Current and future climate and surface hydrologic regimes

NPCTR watersheds can generally be classified by flow regime (figure 4; Fleming et al. 2007, Sergeant et al. 2020). Lower elevation watersheds, where rain is the primary form of precipitation, exhibit low flows in late summer (July–September) with peaks in mean monthly discharge in late fall and early winter (October–December). Higher elevation drainages have hybrid snow- and rain-driven regimes, where flows peak in fall and early winter from rain and rain-on-snow events and again in the spring with melting of seasonal snowpacks. Discharge in both systems tends to be flashy, and flood events are associated with frontal storms originating from the Pacific Ocean. In the highest elevation watersheds, especially in the perhumid NPCTR, snow and ice melt become a dominant source of runoff, with the highest monthly flows occurring in late spring to late summer and low flows in the winter (Moore et al. 2009, Sergeant et al. 2020).

Against a background of naturally high interannual variability associated with coordinated patterns of atmosphere–ocean circulation such as El Niño–Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO), which show differential streamflow effects depending on local hydrologic regime (Fleming et al. 2007), long-term global climate change is altering overall NPCTR hydroclimatology. Continued temperature increases contribute to glacier recession (Larsen et al. 2015) and eventual declines in glacial runoff (Moore et al. 2009), as well as cool-season precipitation increasingly falling as rain rather than snow (McAfee 2013), producing decreased low- to mid-elevation seasonal snowcover.

A major ongoing hydrologic impact of these changes is the shift in geographic distribution of flow regimes, with the extent of rain-driven and hybrid systems moving north and east (figure 4). With a larger proportion of rain relative to snow in winter, more precipitation runs directly into stream channels (particularly in rain-on-snow events), increasing winter streamflow and making channel-changing flows more frequent. Snowpack is reduced, and the snowmelt freshet occurs earlier and is smaller, with a decrease in late summer–early autumn water levels (Shanley et al. 2015). In many northern NPCTR headwater basins, glacial recession is further altering the hydrologic cycle by generating a transitory meltwater pulse that may last for decades, whereas, in southern areas, the loss of glacial ice available for seasonal melt has resulted in an ongoing decline in summer flows, exacerbating effects of diminishing snowmelt and changing downstream biogeochemistry (Hood and Berner 2009, Moore et al. 2009). Collectively these changes in seasonal flows, temperature, and chemistry can have compounding and complex effects on estuarine processes and phenology (Ward et al. 2020).

Although broad impacts of climate change in the NPCTR are well understood, particularly as they relate to temperature-induced shifts, uncertainty remains around details (figure 5). Predicted shifts in precipitation depend on the specific models, data sets, and measures considered; however, a common theme is the likely presence of north–south gradients across the NPCTR. For example, atmospheric river frequency may be increasing across the NPCTR, but the effect might be more pronounced in the north (Payne et al. 2020). There are also potential increases anticipated in summer drought throughout the NPCTR (Mote and Salathe 2010, Walsh et al. 2014, Lader et al. 2020). It remains unclear how ENSO and PDO will be affected by climate change; even without alterations to these climate processes themselves, however, their interactions with the watershed hydrologic cycle will shift fundamentally under climate change, particularly in northern NPCTR streams, where specific interactions between these climate modes and glacial melt runoff will fade as glaciers recede (Fleming et al. 2016).

Terrestrial production and delivery of materials to surface waters

Although coastal rainforest predominates in the NPCTR, the heterogeneity of topography, climate, and disturbance histories across the terrestrial landscape leads to high variation in both the composition and structure of ecosystems, as well as their response to perturbation.

Aboveground stocks and processes. Vegetation in the perhumid NPCTR is a mix of upland coniferous forests and open or forested wetlands, with slope and associated depth to groundwater determining vegetation type and aboveground biomass (Asada et al. 2003, Bisbing et al. 2016). Upland forests predominate in the seasonal NPCTR, where soils tend to be better drained. Across the NPCTR, aboveground C storage is high compared with tropical and boreal forests (Keith et al. 2009), estimated from 325 Mg per ha (95% confidence interval [CI]= 50) at the northern end (Alaska; Leighty et al. 2006), and increasing southward to 455 Mg per ha (95% CI = 156; BC; Matsuzaki et al. 2013) and 685 Mg per ha (95% CI = 47; Oregon and Washington; Smithwick et al. 2002). Forests of the NPCTR have been a relatively stable, large C sink over the past several decades (Peng et al. 2014, Buma and Barrett 2015), but sensitivity to climatic and hydrologic forcing means that thresholds in C production and storage are likely to be crossed as the climate continues to change.

Forest C stability is driven largely by a conspicuous lack of frequent, large-scale or high-severity disturbances, particularly in the perhumid NPCTR. The infrequency of disturbances (0.03%–0.84% area disturbed per year, 2000–2012; Buma et al. 2017) combined with the longevity of many dominant tree species (often more than 500 years; Waring and Franklin 1979) means that, at broad temporal and spatial scales, materials export from forests to streams generally depends on climatically mediated changes in the hydrologic cycle itself. Increasing disturbance frequency may, however, have a negative effect on soil C stocks and stability because of disruption of the soil profile, alteration of infiltration and drainage, and changes in species composition (Defrenne et al. 2016). Summer drought is driving increases in fire prevalence and extent in portions of the NPCTR, where this disturbance was historically infrequent (Reilly et al. 2017) and increases in fire severity in areas in which fire was already important historically (Schoennagel et al. 2017). Fires strongly affect the C cycle and could change the region from a C sink to source and lead to increasing water flux through forested ecosystems (e.g., Buma and Livneh 2017). Shifts in forest C stocks and greater C delivery to surface waters are also likely with the increase in frequency and severity of mass-movement disturbances, such as windthrow and landslides, predicted with climate-mediated changes in weather patterns (Dale et al. 2000).

With or without dramatic shifts in disturbance regimes, C sequestration and storage will be affected as the distributions (Hamann and Wang 2006) and growth (Buma and Barrett 2015) of tree and shrub species change under altered precipitation and temperature regimes. Changes in landscape-scale forest biomass consistent with a warming climate are already apparent across the Alaskan NPCTR, with increases on northerly aspects, at lower elevations, and at higher latitudes (Buma and Barrett 2015). Future warming that reduces energy limitations will likely result in continued increases in forest growth in the perhumid NPCTR, whereas intensified summer drought may decrease tree establishment and growth rates in the seasonal NPCTR (Kang et al. 2014).

Although C storage is a key focal point in the carbon-dense NPCTR, coupled aboveground and belowground changes to other elemental cycles (i.e., N and P) are also predicted as climate and disturbance regimes change. More frequent freeze–thaw events associated with warming winters can alter couplings between plant nutrient uptake, microbial communities, and nutrient cycling that ultimately lead to increased soil N and the potential for P leaching (Wipf et al. 2015). Freeze–thaw events associated with transitions from snow to rain are additionally driving sudden shifts in forest community composition (e.g., yellow cedar *Callitropsis nootkatensis* replacement by western hemlock *Tsuga heterophylla*; Oakes et al. 2014, Bisbing et al. 2019). These shifts can in turn influence soil N cycling rates (Bisbing and D'Amore 2018) although total nutrient stocks may change more slowly. Disturbance events may also greatly alter N availability and loss via vegetation change. For example, the widespread symbiotic nitrogen-fixing tree red alder (*Alnus rubra*) is favored by both fire (Long and Whitlock 2002) and projected climate change (Cortini et al. 2012), with the potential to greatly increase watershed N export (Compton et al. 2003). Overall, the relationship between these anticipated changes in aboveground productivity and community composition and materials export is not well constrained and it remains unknown how it may vary across the region (figure 5).

Belowground stocks and processes. Across the NPCTR, wetlands store exceptional amounts of belowground C—up to 709 Mg per ha in peatlands (McNicol et al. 2019) and 822 Mg per ha in tidal forested wetlands (Kauffman et al. 2020), and when combined with aboveground C, these forest and wetland ecosystems store some of the highest amounts of C per unit area globally (Keith et al. 2009). The cool climate and persistent soil saturation of the perhumid, and to a lesser extent seasonal, NPCTR create unfavorable conditions for decomposition, supporting the accumulation of substantial soil C stocks. High soil C stocks in turn facilitate storage of organic forms of N and P in soil (Perakis et al. 2017, Kranabetter et al. 2020), with particularly rapid C, N, and P increases under N-fixing red alder (Dynarski et al. 2020).

The flow of water both vertically and laterally through NPCTR soils is a fundamental control on the production, cycling, and export of materials across the terrestrial–aquatic interface. Both deep, well drained and shallower, poorly drained NPCTR soils display high C and nutrient storage potential, but export potential depends greatly on soil hydrology. For instance, persistent soil saturation in the abundant wetlands in the perhumid NPCTR mobilizes DOC and transports it laterally to streams while also increasing anoxic soil conditions that restrict oxidized nutrient forms (e.g., nitrate [NO_3^-]) in soil water (Emili and Price 2013, D'Amore et al. 2015b). High biotic demand for nutrients further suppresses inorganic pools (Bisbing and D'Amore 2018) and results in organic nutrients as the dominant export to surface waters (Fellman et al. 2008, Hood et al. 2019). On the other hand, vertical water flow through deep, well-drained soils of the seasonal NCPTR increases DOC sorption onto mineral soil horizons and reduces DOC available for transport to surface waters (Cory et al. 2004). High soil N content can simultaneously cause natural N-saturation and high N export as NO_3^- in watersheds with high alder coverage, despite low atmospheric N deposition (Perakis and Sinkhorn 2011). These differing soil biogeochemical and hydrologic properties across the NPCTR create exceptional ranges of potential C and nutrient delivery to surface waters, and their collective implications across the landscape are not well understood (figure 5).

Hydrologic regimes additionally influence soil biogeochemical transformations via seasonal water table drawdown and soil moisture depletion driven by high evapotranspiration and lower precipitation in spring and early summer. This seasonal drought depresses water table levels and expands the aerobic zone into the hydrologically inactive subsurface horizons, facilitating organic matter mineralization (Emili and Price 2013, D'Amore et al. 2015b) and the accumulation of OC and nutrients (N, P, and silicon) in the shallow subsurface soil layers (Ward et al. 2012). Subsequent rainfall that elevates water table levels into the highly conductive surface horizons facilitates lateral transport of OC and nutrients to surface waters. The largest lateral OC and nutrient fluxes occur episodically when rainfall is preceded by warm, dry periods that allow for water table drawdown and enhanced soil C mineralization (e.g., Fellman et al. 2009, Ward et al. 2012). Therefore, extension of the summer seasonal drought may increase fall-season OC flux to surface waters.

The overarching influence of temperature and watershed hydrology as drivers of materials generation, processing, and delivery affirms that climate-driven changes will have significant impacts on export of terrestrial-derived materials to coastal ecosystems. Increased terrestrial ecosystem productivity in response to warmer temperatures, for instance, is likely to increase net C inputs to soils in the perhumid NPCTR (McGuire et al. 2018), while, at the same time, warmer temperatures may increase soil OC decomposition (Fellman et al. 2017). This will likely lead to enhanced C generation and export, although the magnitude and dynamics of changes depend on how C transport is affected by hydrologic regime shifts and the ability of soil microbes to remove DOC before delivery to surface waters (figure 5; Jepsen et al. 2019). Furthermore, study is needed to parse out the relative importance of these drivers on C flux and how this scales across the region.

Materials export to the coastal ocean

Material fluxes from NPCTR streams to the ocean are substantial, although, to date, there has been more emphasis on C flux (mainly DOC) than other elements. In the Alaskan NPCTR, the estimated areal hydrologic C flux rate is nearly five times the mean areal flux for the conterminous United States (Butman et al. 2016), and the total DOC flux is 17%–20% of that from the conterminous United States (Edwards et al. 2020). Forested streams across the NPCTR have variable but relatively high concentrations of DOC (approximately 1 to 25 milligrams of C per liter), which, in combination with high rates of specific discharge, result in yields of DOC more than 20 grams of C per square meter per year from small, coastal watersheds in Alaska and northern BC (D'Amore et al. 2015a, Oliver et al. 2017). These are among the highest measurements recorded worldwide. In the southern NPCTR, DOC yields are generally lower (approximately 2 grams of C per square meter per year) as a result of the predominance of water flow through DOC-sorbing mineral soils (Cory et al. 2004) and lesser prevalence of wetlands on the landscape. Although concentrations of DOC are low under glacial influence (Hood and Scott 2008, Fellman et al. 2014), absolute fluxes of DOC from glacial rivers can be substantial because of the high specific discharge associated with glacial watersheds (Hood et al. 2009). This range of behaviors illustrates how understanding of climate drivers and climate change affects materials flux across the NPCTR can broadly inform patterns and processes in other regions globally.

Fluxes of riverine dissolved inorganic C (DIC; as carbon dioxide [CO_2] and bicarbonate) and riverine particulate organic C (POC) are poorly quantified for the NPCTR. However, a study in the Eel River, California, found that DIC varied markedly with streamflow (Finlay 2003), suggesting a vulnerability to change with future hydrologic regimes. The few studies of riverine POC export indicate that concentrations are higher in the wet winter months in southwestern BC (Kiffney et al. 2000), whereas export is dominated by short-lived, high discharge events in coastal Oregon and California (Goñi et al. 2013, Thom et al. 2018). In fact, recent research in a small headwater stream in Oregon suggests that POC yields can be twice that of DOC (Argerich et al. 2016), highlighting the potential importance of POC to total aquatic C flux; however, this may not hold true for perhumid watersheds rich in DOC. Riverine DIC in the region is further substantially enhanced by the action of glaciers (Anderson et al. 2000), and glacial runoff (especially in Alaska and BC) also likely plays an important role in POC export, as has been documented in other glacierized regions (Bhatia et al. 2013).

Beyond C, the export of N, P, Fe and other micronutrients is not well quantified for the NPCTR. This is especially true for the thousands of small, ungauged rivers in BC and Alaska, although limited studies suggest that organic N and P yields dominate total N and P export in the north (Hood et al. 2019). Inorganic nutrient forms dominate N export along the coastal margin from Washington to northern California, which is likely because of local areas of agricultural fertilizer runoff, and more broadly, the abundance of N-fixing alder (Compton et al. 2020). Maximum export of trace metals (e.g., Fe and manganese) has been shown to occur during periods of high flow when dissolved organic matter (DOM) loads are high, as a result of organic-matter–metal interactions (Sugai and Burell 1984). In addition, glacial streams are characterized by high levels of glacier-derived silt and elevated fluxes of rock-derived nutrients such as P and Fe relative to forested watersheds (Hood and Berner 2009). Spawning salmon also seasonally release large quantities of inorganic N and P and thereby contribute to seasonal watershed nutrient yields (Hood et al. 2019). Further effort is needed to constrain nutrient export across space, season, and storm event cycles in the NPCTR (figure 5).

Influences of materials export on coastal marine ecosystems

Physical processes and nutrient subsidies driven by freshwater fluxes maintain tight links between terrestrial and marine environments in the NPCTR. Riverine discharge plays an important role in the supply of nutrients to the continental shelf off of southern BC, Washington, and Oregon through its influence on coastal circulation (Davis et al. 2014). Northward, terrestrially derived Fe and associated nutrients are transported off the shelf into the GOA by large, low-salinity eddies driven by coastal currents (Ladd et al. 2009). In the high NO_3^- and Fe environment of the GOA, these Fe subsidies in particular can significantly enhance primary productivity (Boyd et al. 2007), which highlights the importance of land-to-ocean links in coastal margin productivity.

Closer to shore, the thousands of relatively small and steep NPCTR watersheds support rapid delivery of freshwater, C, and nutrients to nearshore environments with minimal time for microbial processing while in the freshwater environment (Oliver et al. 2017). Although terrigenous N delivered by rivers is likely insignificant in the context of the greater continental shelf and North Pacific marine ecosystem

(Brown and Ozretich 2009, Sutton et al. 2013), it may be locally important to estuarine and nearshore habitats. Along the Oregon coast, high freshwater silicate and nitrate (NO_3^-) loads delivered from small coastal rivers during storms can promote winter phytoplankton production and deliver sufficient Fe to support the entire summer upwelling production (Wetz et al. 2006). In addition, high organic matter (OM) loads may stimulate seasonal microbial productivity, which enhances OM mineralization and release of inorganic nutrients that likely play a key role in making terrestrial nutrients accessible to marine food webs (Fellman et al. 2010, St. Pierre et al. 2020). Stable and radiogenic C isotopic analyses have demonstrated incorporation of terrestrial OM by higher trophic level pelagic organisms such as fish and seabirds in coastal Alaska and the seasonal NPCTR (Maier and Simenstad 2009, Arimitsu et al. 2018). Overall, the pathways of terrestrial OM assimilation into NPCTR marine food webs are not well characterized, although it is expected that accessibility is mediated by the quality and bioavailability of the terrestrial OM (figure 5; Bianchi 2011).

The potential shift toward warmer, wetter winters and drier summers under a changing climate is expected to alter the timing and intensity of marine–terrestrial links, particularly in the perhumid NPCTR. A weakening of the spring freshet in glaciated fjords may in turn weaken summer estuarine circulation and nearshore nutrient resupply to these ecosystems (Davis et al. 2014). High winter freshwater discharge has been linked with decreased primary production because of intensification of summer stratification (Thomson et al. 2012). This was proposed to be the mechanism behind the exceptionally low marine survival of Fraser River sockeye in 2007, yielding a 2009 return that was the lowest on record at that time (McKinnell et al. 2014).

The large inputs of freshwater and terrestrial C (organic and inorganic) also influence the coastal ocean C and carbonate systems. The marine waters of the NPCTR have a natural tendency to conditions corrosive to carbonates (Feely et al. 2008), and this can be locally enhanced by freshwater outflows such as glacier meltwater that is undersaturated in CO_2 compared with the atmospheric reservoir (Reisdorph and Mathis 2014). Changes in the delivery of this lower alkalinity water are expected to affect the timing and intensity of ocean acidification as well as hydrodynamics on and off the shelf (Siedlecki et al. 2017). Small changes in ocean pH may have large impacts on coastal food webs, especially food web components (e.g., pteropods, bivalves, and crustaceans) that depend on calcium carbonate (Haigh et al. 2015). Future research should investigate how natural variability in the carbonate chemistry of NPCTR coastal waters will be affected by changes in C biogeochemistry and freshwater runoff, and their interaction with increases in atmospheric CO_2.

Advancing knowledge in coastal temperate rainforest ecosystems

Despite the recent research into aspects of the NPCTR ecosystem, significant knowledge gaps—such as those described in the preceding sections—remain in our understanding of the interconnected processes across CTR margins, in the NPCTR and globally (figure 5). For example, although there are regional estimates of OC stocks and aquatic fluxes (mainly DOC), fundamental uncertainties persist regarding overall vulnerability of the NPCTR C stock to climate change; the export (quantity and timing) of N, P, Fe, and other micronutrients; the pathways of terrestrial materials incorporation into marine food webs; and the spatial variability in these processes across scales from watersheds to the region. Because of the complex interplay between systems that are traditionally studied by disparate disciplines, the cumulative effects governing the magnitude, scale, and timing of freshwater and materials flux to NPCTR coastal ecosystems remain poorly understood. Nonetheless, the NPCTR represents a useful study system for testing hypotheses regarding the importance of materials production and export from coastal watersheds to the nearshore marine ecosystem and how these links might change with future climate conditions. In particular, the differences between the perhumid and seasonal NPCTR subregions—in coastal morphology and complexity, number and size of coastal watersheds, upwelling versus downwelling, disturbance regimes, and distribution of wetlands—superimposed on regional gradients in precipitation and temperature provide opportunities for comparative work into the sensitivity of ecosystem processes and threshold responses across this coastal margin. Such studies across broad geomorphic and environmental gradients could also inform understanding in other coastal margins that share features of the NPCTR (figure 1).

There are, of course, limits to this approach across major ecosystem domains. The production, mobilization, and export of materials through the NPCTR are affected by highly variable seasonal and interannual climate forcing, making it difficult to unravel climate-induced changes in terrestrial-to-marine links from the natural variability that defines the region. However, in our view regional spatial comparisons will nevertheless provide insight into the ecosystem functions of major domains, their geography, and transitional zones while improving the science basis of predictive Earth systems modeling (Ward et al. 2020). Therefore, using the natural variability inherent across the NPCTR for comparative studies, we recommend the prioritization of the following research themes (figure 1), which are also relevant to other CTRs around the world:

Will the terrestrial ecosystems of the NPCTR become a source or sink of C under a changing climate? Changes to tree growth, species distributions, and disturbance patterns across the region complicate projections of total ecosystem C stocks, and trajectories may be different in the north versus the south. For belowground stocks, laboratory incubations show that NPCTR wetland soils contain a sizeable pool of readily biodegradable OC that can be mineralized to CO_2 or lost as DOC via leaching and lateral export with future climate warming (Fellman et al. 2017). These results,

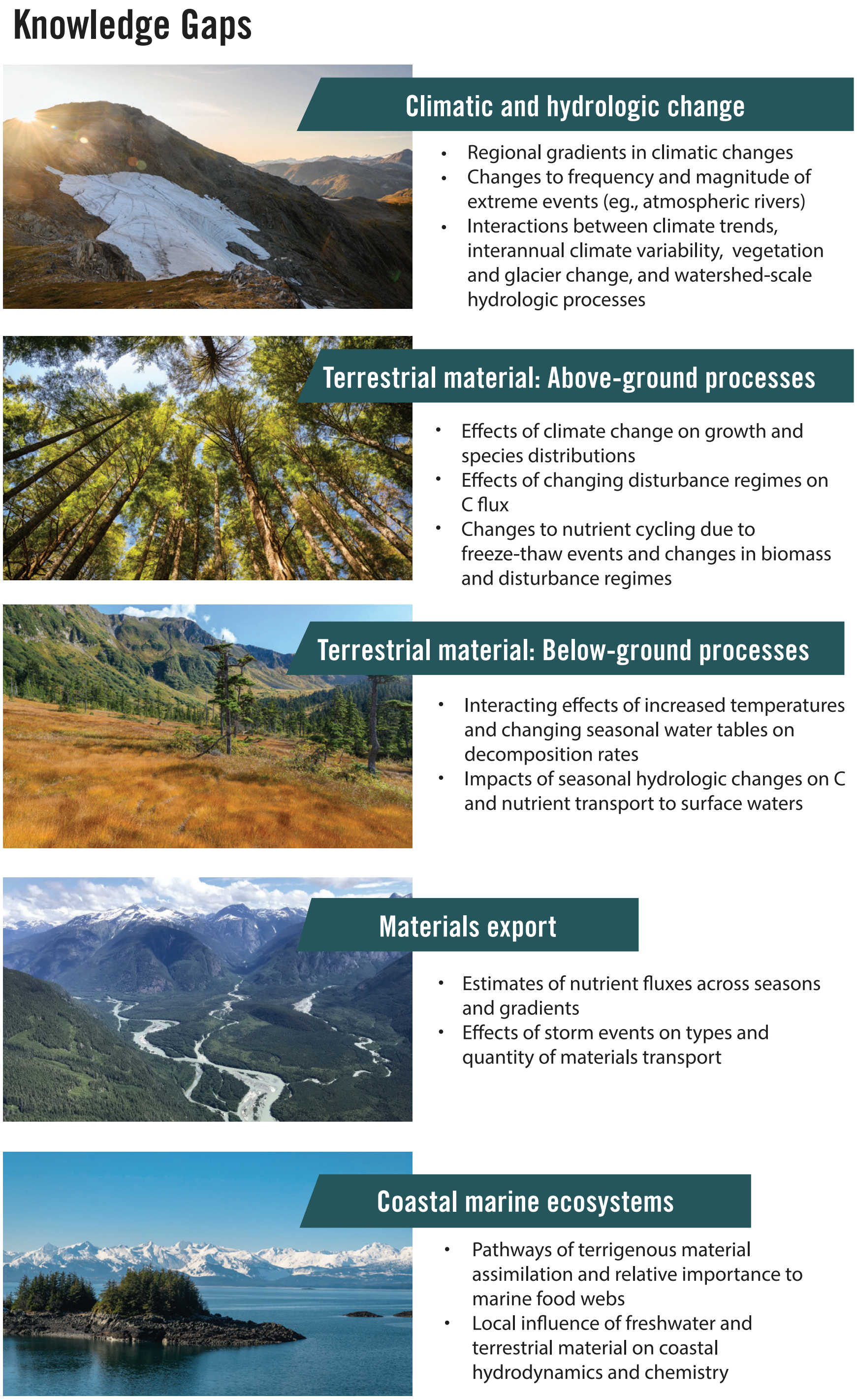


Figure 5. Knowledge gaps in NPCTR ecosystem processes as was discussed in the text. Characteristic landscape types in the NPCTR from top to bottom: hanging glacier, Alaska (photograph: Molly Tankersley); upland forest, Alaska (photograph: Molly Tankersley); sloping fen wetland, Alaska (photograph: Molly Tankersley); glacially carved valley, British Columbia (photograph: Ian Giesbrecht); mountainous coastal landscape, Alaska (photograph: Molly Tankersley).

combined with paleo records of long-term C accumulation in peatlands (Turunen and Turunen 2003), suggest that, under future climate regimes, perhumid NPCTR soils may transform from an ecosystem that suppresses organic matter decomposition and sequesters C to one that promotes more vegetation production and enhanced decomposition. These changes may be less pronounced in the seasonal NPCTR given already warm summer temperatures and little precipitation, where instead climate-mediated changes in wildfire regimes could greatly influence ecosystem C balances. Better estimates of plant growth and especially mortality (Harmon and Bell 2020) across the region are needed to project changes in aboveground biomass accumulation, and field measurements of soil C turnover or manipulative studies of temperature and water table are clearly necessary to assess the vulnerability of the region's massive soil C stock to climate change.

How will predicted climate changes influence the land-to-ocean movement of freshwater and materials? Climate instability in the NPCTR, which may manifest through changes to mean hydroclimatic regimes and more extreme weather events such as winter storms and summer drought, will affect terrestrial production, removal, and export of materials to the marine ecosystem. Warmer temperatures, longer periods of summer drought, and lowering of the soil water table drive organic matter decomposition. Lower winter snowpacks and consequent freezing soil conditions may lead to seasonal increases in soil DOC concentrations (Haei et al. 2013). When these periods are followed by severe storms, massive amounts of OC and nutrients may be transported laterally into stream networks and flushed to the ocean (e.g., Fellman et al. 2009). Severe storms can also lead to landslides and other mass wasting events, moving large volumes of rock and OM downstream (Swanson and Lienkaemper 1978, Guthrie et al. 2010). Whether these types of events lead to an overall increase in materials transport or simply a change in the frequency, amplitude, timing, and seasonality of fluxes is unknown.

What regime shifts and nonlinearities will dominate NPCTR ecosystem dynamics under continued climate change? Transitions from snow-dominated to rain-dominated precipitation regimes along both latitudinal and elevational gradients are leading to rapid changes in both forest community composition and the timing of runoff, two seemingly discrete but tightly connected components of this system. In addition, rising temperatures and increasing summer droughts are leading to increasing severity and extent of wildland fires. We have only a poor understanding of the extent to which these shifts will lead to abrupt changes in biogeochemical cycling and export across the coastal margin, i.e., thresholds and new stable states (Groffman et al. 2006), and if so, how that may differentially manifest in the perhumid versus the seasonal NPCTR. For example, will changes in forest C storage be gradual—with gains and losses correlated with temperature, precipitation, and topography (Buma and Barrett 2015)—or episodic as fire increases in severity and drives rapid shifts in composition and functioning (Gavin et al. 2013)? Comparative studies across the region are needed to better understand the rate and magnitude of ecosystem change given ongoing and future climate trajectories.

How will key links among NPCTR ecosystem components strengthen or weaken with continued climate change? Within the NPCTR, there may be distinct places and times at which the magnitudes of biogeochemical processes are sufficient to influence entire ecosystems (i.e., ecosystem control points; Bernhardt et al. 2017), but these have not been identified or characterized for this region. For example, we hypothesize that the strength and magnitude of coastal hydrodynamic phenomena such as the Riverine Coastal Domain may become more variable in response to changing weather patterns and hydrologic regimes, affecting the marine transport and processing of terrestrially derived materials. Similarly, altered disturbance regimes may influence water, C, and N fluxes from terrestrial to freshwater ecosystems, strengthening the links within watersheds. Collection of baseline data, long-term monitoring, comparative studies, and modeling are necessary to investigate how the strength of terrestrial–marine connections is likely to be altered.

What is the relative importance of terrestrially derived materials in regulating marine ecosystem processes in the NPCTR and how will marine ecosystems respond to altered land-to-ocean materials fluxes? Climate-mediated alteration of freshwater discharge will affect coastal currents, sea surface temperature, and the delivery (timing and concentrations) of materials to the ocean, potentially affecting phenology and productivity of lower trophic levels in the nearshore and beyond the continental shelf. For example, in the perhumid NPCTR, increased glacial melt and stronger storms may deliver more DOC to the coastal ocean, favoring bacterioplankton over phytoplankton and potentially altering marine food webs (e.g., Andersson et al. 2018). More information about elemental production and delivery to freshwaters and the processing of materials by marine microbes in the water column, at the sediment–water interface, and in sediment is needed. Studies that pair measurements of OM flux and bioavailability with quantification of estuarine metabolism will allow us to constrain the contribution of terrestrial-derived OM to estuarine demand.

Conclusions

These research themes are useful as a framework for investigating terrestrial–marine links in other CTRs and coastal systems around the world. To date, there has been very little comparative work among CTRs even though these regions exhibit similar climates, ecosystem functioning, and materials fluxes. How do NPCTR ecosystem processes compare with other CTRs, such as in Chile and New Zealand? Studies into the role of storms in nutrient export, the burial of C versus assimilation by marine microbes, and the importance of seasonality in the timing of materials fluxes on coastal processes have the potential to provide insights into the collective impact of such high-flux ecosystems on global elemental cycling. Similarly, studies of the production, removal, delivery, and fate of materials within CTRs may be valuable in advancing our understanding of ecosystem connections across a variety of coastal margins (e.g., Marcarelli et al. 2018), and in creating better predictive models of such links.

Like CTRs worldwide, the NPCTR expresses regionally consistent patterns of forest cover, extremely high precipitation and runoff, and proximity to the coast. But within these broadly consistent patterns, it is spatially divided at a large scale by physiography and glacial history and at a finer scale by highly dissected topography and associated microclimates, and variable physical processes and ecological responses stratified along latitudinal and elevational gradients. At more than 2000 km in length, the NPCTR spans four U.S. states and a Canadian province, and this transnational character combined with its relative remoteness to large urban centers may have contributed to its lack of prior holistic study as a unified rainforest ecosystem. With climate-driven changes to watershed hydrology and above- and belowground ecological processes combining to alter the magnitude, timing, and type of materials flux into nearshore marine systems, there is a pressing need to bridge prior divides across disciplines and research traditions. Doing so will provide insight into the importance and sensitivity of processes linking terrestrial and marine ecosystems around the world.

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