Anticipating Stream Ecosystem Responses to Climate Change: Toward Predictions that Incorporate Effects Via Land–Water Linkages

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ABSTRACT

Climate change (CC) is projected to increase the frequency and severity of natural disturbances (wildfires, insect outbreaks, and debris flows) and shift distributions of terrestrial ecosystems on a global basis. Although such terrestrial changes may affect stream ecosystems, they have not been incorporated into predictions of stream responses to CC. Here, we introduce a conceptual framework to evaluate to what extent responses of streams to CC will be driven by not only changes in thermal and hydrologic regimes, but also alterations of terrestrial processes. We focused on forested watersheds of western North America because this region is projected to experience CC-induced alteration of terrestrial processes. This provided a backdrop for investigating interactive effects of climate and terrestrial responses on streams. Because stream responses to terrestrial processes have been well-studied in contexts largely independent of CC research, we synthesized this knowledge to demonstrate how CC-induced alterations of terrestrial ecosystems may affect streams. Our synthesis indicated that altered terrestrial processes will change terrestrial–aquatic linkages and autotrophic production, potentially yielding greater sensitivity of streams to CC than would be expected based on shifts in temperature and precipitation regime alone. Despite uncertainties that currently constrain predictions regarding stream responses to these additional pathways of change, this synthesis highlighted broader effects of CC that require additional research. Based on widespread evidence that CC is linked to changing terrestrial processes, we conclude that accurate predictions of CC effects on streams may be coupled to the accuracy of predictions for long-term changes in terrestrial ecosystems.

Key words: food web; wildfire; disturbance; indirect effects; forest cover.

INTRODUCTION

Understanding the ecological consequences of climate change (CC) will require approaches that encompass possible feedbacks and interactions between stressors, as these may influence the

magnitude and direction of CC effects. For example, when responses of vegetation and disturbance regimes to CC are not integrated into predictive models, they may under- or overestimate projected air temperature increases due to CC (Goetz and others 2007; Kurz and others 2008). Wildfires in particular may create negative feedbacks to CC, because they can convert coniferous forests to grasslands or deciduous forests, subsequently increasing albedo (Goetz and others 2007). Conversely, vegetation changes due to insect outbreaks or fire can reduce carbon storage, creating positive feedbacks to CC (Goetz and others 2007; Kurz and others 2008). Because organisms in a range of terrestrial, freshwater, and marine ecosystems have exhibited sensitivity to warming (Rosenzweig and others 2008), such interactions that amplify or dampen expected temperature shifts will likely have additional consequences for accurate forecasting of ecosystem responses to CC.

Stream ecosystems are likely to be affected by CC-induced shifts in temperature and precipitation regimes, but other ecological factors may alter these responses. In terms of temperature and precipitation effects, many stream biota are sensitive to thermal change (Thackeray and others 2010) and have adapted to past flow regimes that may shift with CC (Poff and others 2010). Due to most CC research focusing on responses to changing temperature and flow, there is ample evidence that CC may alter aquatic species phenologies (Thackeray and others 2010), distributions (Sweeney and others 1992; Wenger and others 2011), and interactions (Woodward and others 2010). However, CC is occurring simultaneously with other ecological changes (nutrient enrichment and land-use change) that also affect streams and may magnify or attenuate stream responses to CC (Kaushal and others 2010; Moss 2010). For instance, rising air temperatures have coincided with stream warming throughout North America, but stream temperature increases have occurred more rapidly in urban watersheds, presumably due to interactions with land-use change (impoundments and loss of canopy cover; Kaushal and others 2010). Simultaneous nutrient enrichment and warming also led to hypoxia and increased fish mortality beyond what was expected based on such changes alone (Moss 2010). Thus, there is building evidence that the predicted effects of CC could be over- or underestimated without considering the broader-scale ecological context in which changes are occurring.

Stream responses to CC may be underestimated if predictions do not incorporate consequences of shifts in terrestrial ecosystem structure and disturbance regimes (frequency and magnitude of wildfires, insect outbreaks, and drought) that are accompanying CC (Pierce and others 2004; Bentz and others 2010; Westerling and others 2011). It is a foundation of stream ecology that terrestrial and stream ecosystems are linked via light flux and inputs of nutrients, sediment, and organic matter; thus, changes to terrestrial ecosystems can affect streams (Likens and Bormann 1974; Hynes 1975). In principle, then, even small alterations of terrestrial ecosystems may affect stream responses to CC (Ball and others 2010). For instance, warming related to CC is expected to facilitate the spread of hemlock woolly adelgid beetles (*Adelges tsugae*), subsequently increasing mortality of eastern hemlocks (*Tsuga canadensis*) in North America (Dukes and others 2009). This may elicit the functional disappearance of a dominant riparian species, with consequences for biogeochemical cycling in streams (Ellison and others 2005).

Shifts in terrestrial disturbance regimes by CC will likely change stream ecosystems as well. For instance, wildfire and fire-related debris flows (liquefied landslides that erode hillslopes and scour stream channels) can remove canopy cover, which in turn can increase light flux, warm streams, and affect stream biota (Dunham and others 2007; Romme and others 2011). Also, increases in such disturbance that may accompany CC are projected to alter species ranges, forest assemblages, and ecosystem boundaries in regions worldwide (Shafer and others 2001; Williams and Jackson 2007; Frelich and Reich 2010). Between 10 and 50% of global land area is highly vulnerable to CC and may exhibit shifts in ecosystem distributions up to 400 km in latitude (Gonzalez and others 2010). Thus, some forest ecosystems may be converted to shrub-grasslands and some tundra ecosystems may be converted to forest (Shafer and others 2001; Frelich and Reich 2010; Gonzalez and others 2010). Given evidence linking CC with shifts in terrestrial processes (disturbance regimes and ecosystem structure) that can alter stream ecosystems, effects of CC on streams may be over- or underestimated without considering such interactions.

Currently, there are few CC studies upon which to develop predictions that integrate stream responses to a combination of CC-induced shifts in precipitation, temperature regimes, and terrestrial processes. However, that does not mean there is no basis for generating such predictions. There is a rich history of research on linkages between stream and terrestrial ecosystems (Likens and Bormann 1974; Hynes 1975). The effects of altered terrestrial
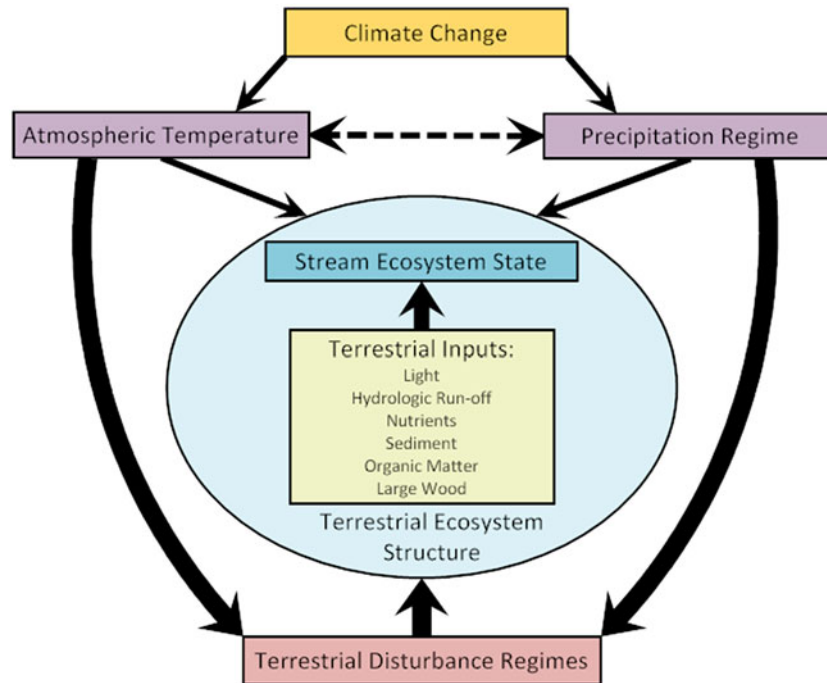
Figure 1. Conceptual diagram indicating the pathways by which climate change may alter stream ecosystem structure and function (ecosystem state). Climate change will alter temperature and precipitation regimes, with consequences for streams. However, shifts in temperature and precipitation regimes will increase the frequency and spatial extent of terrestrial disturbances (drought, wildfire, debris flows, biological invasions, and insect outbreaks) that will change terrestrial ecosystem structure. In turn, this will alter terrestrial inputs to streams (water run-off, nutrients, sediment, light, and organic matter), with consequences for stream ecosystem state. *Arrow* widths are proportional to expected effects. *Dotted arrow* indicates interactions between air temperature and precipitation responses.

processes on streams have been well-studied, albeit in contexts largely independent of CC (wildfire and deforestation; Gresswell 1999; Kiffney and others 2003). Assessment of their importance has begun in the arctic where thermal increases may be greatest. For instance, positive effects of warming on stream production may be partly offset by concomitant increases in sedimentation due to permafrost thawing and hillslope failure (Bowden and others 2008). Similar interactions may occur in temperate biomes, but research has largely focused on effects of changing temperature and flow without explicitly integrating impacts of altered terrestrial processes (Poff and others 2010; Woodward and others 2010). Yet, by leveraging existing knowledge, we can begin to anticipate how similar CC-induced shifts in such processes may alter stream structure and function.

Objectives

Here, we introduce a conceptual framework regarding the long-term effects of CC on forested temperate streams. It not only encompasses effects of CC on temperature and flow regime shifts, but also integrates effects of CC-induced alteration of terrestrial disturbance regimes (drought, wildfires, insect outbreaks, and debris flows) and ecosystem distributions (Figure 1). Building from this conceptual framework, we conducted a synthesis of relevant literature using a qualitative model approach (Levins 1966), a useful technique for investigating responses of ecosystems to perturbation when the magnitudes of many parameters are unknown (Justus 2005). We integrated stream ecology literature from outside the realm of CC research (Likens and Bormann 1974; Ball and others 2010) and beyond our focal region (Ball and others 2010) when these helped predict in general how streams may respond to terrestrial ecosystem changes. Through this synthesis we evaluated the extent to which predicted responses of stream ecosystems to CC-induced thermal and hydrologic regime shifts are changed by incorporating effects that may occur via land–water linkages.

The synthesis was centered on mountainous river basins of western North America, a region in

which stream responses to terrestrial disturbances (wildfire, debris flows, and insect outbreaks) and altered precipitation regimes have been well-studied (see below). First, by reviewing current evidence, we identified changes in terrestrial processes that are occurring in conjunction with CC. For instance, CC is shifting many mountainous regions from a snow- to rain-dominated precipitation regime, subsequently increasing the frequency, severity, and spatial extent of natural disturbances over the time span considered (150–200 years). We selected this time span because in western North America it is comparable to historic fire return intervals (200–400 years) and time required for mixed conifer forests to reach old-growth status (200–500 years; Oliver 1981; Arno and others 1985; Nelson and Pierce 2010). Stream responses may differ over shorter periods (1–10 years), but such transitory effects may not fully reflect responses to climate and terrestrial changes that are occurring over many decades (IPCC 2007; Gonzalez and others 2010). We then demonstrate that greater disturbance activity is predicted to alter terrestrial ecosystem distributions and the structure of dominant ecosystem types drained by river networks. Next, we evaluate how altered terrestrial processes may affect stream flow, temperature, light flux, and inputs of nutrients, sediment, and organic matter. We then discuss potential consequences for stream ecosystems.

We focused on mountainous river basins of western North America that are largely snowmelt-driven and are expected to experience alterations of terrestrial disturbance regimes. However, we expect that the conceptual framework (Figure 1) will be applicable to other regions because CC-induced alterations of hydrology, terrestrial disturbance regimes, and ecosystem boundaries are predicted worldwide (Barnett and others 2005; Bentz and others 2010; Gonzalez and others 2010; Moritz and others 2012). Drought has increased tree mortality in a range of ecosystems on all forested continents (Allen and others 2010). Similarly, wildfire activity is increasing globally (Moritz and others 2012). For instance, wildfire area may increase 3–5 times in the Mediterranean (Dury and others 2011) and 2 times in boreal forests (Flannigan and others 2009), with implications for vegetation structure (Malkisnon and others 2011; Wolken and others 2011). Also, CC is expected to increase the extent of insect outbreaks in many regions, such as hemlock woolly adelgid beetles in North America and spruce bark beetles (*Ips typographus*) in Europe (Jonsson and others 2007; Dukes and others 2009). Geographic ranges of species and entire ecosystems are also projected to move due to shifts in climate and disturbance regimes (Williams and Jackson 2007; Gonzalez and others 2010). Finally, human activities and CC may aid the spread of some nonnative species (Walther 2004).

EFFECTS OF CLIMATE CHANGE ON TERRESTRIAL AND STREAM ECOSYSTEMS

Thermal and Precipitation Regimes

Climate models for western North America project a 1–5°C increase in air temperature, increases in winter precipitation, and declines in summer rainfall by 2080 (Mote and Salathe 2010). Such changes will likely affect mountain streams in this region as they typically rely on winter snowpack to sustain baseflow during dry summers (Barnett and others 2005; Stewart 2009). For example, atmospheric warming has reduced snowpack as more precipitation occurs as rain (Knowles and others 2006), which is projected to increase the frequency of winter floods and decrease summer baseflow (Stewart 2009). Warming has also shifted spring snowmelt earlier and reduced the size of spring run-off in this region (Stewart 2009; Kunkel and Pierce 2010). Thus, CC may not affect total annual precipitation, but is expected to change when and how it falls. This may increase the prevalence of winter floods and terrestrial disturbances due to transitions from snowpack accumulation to rain-on-snow events (Figure 1).

Terrestrial Disturbance Regimes

Reduced snowpack and earlier snowmelt in western North America have increased summer drought, the frequency and severity of wildfire (Westerling and others 2006), and fire-related debris flows (Pierce and others 2004). Wildfire area in this region is expected to increase by 54% due to CC, with the Rocky Mountains projected to see some of the largest increases (175%; Spracklen and others 2009), and loss of coniferous forests in some areas by 2050 (Westerling and others 2011). Increased fire will likely be coupled with more frequent debris flows. Debris flows occur in unburned streams, but their magnitude and probability of occurrence increases post-fire (Cannon 2001; Miller and others 2003). For instance, May and Gresswell (2003) found that 54% of streams that were affected by wildfire experienced a debris flow within 30 years of fire, in contrast to 12% of unburned streams; effects were still detectable more than 100 years post-debris flow. Paleoecological records

have found similar relationships between climate, fire, and debris flows (Pierce and others 2004), indicating that current warming also may increase their frequency (Figure 1).

Drought can increase vulnerability of trees to insect infestations (Dukes and others 2009; Bentz and others 2010). Warming of 1–2°C has increased the frequency of large insect outbreaks in high latitude and elevation habitats that previously did not experience them (Raffa and others 2008). Even in areas where outbreaks occurred historically, they persist longer due to successive warm summers that stimulate insect reproductive cycles and warmer winters that minimize cold-induced mortality (Raffa and others 2008; Bentz and others 2010). In particular, mountain pine beetle (*Dendroctonus ponderosae*) outbreaks over the past decade have affected greater than 25 million ha throughout western North America, with future increases projected (Bentz and others 2010).

Terrestrial Vegetation Structure

Higher atmospheric temperatures and CO_2 concentrations are projected to increase plant production, but effects may attenuate over longer-time scales (Norby and others 2010; Wu and others 2011). For instance, Norby and others (2010) found that CO_2 enrichment initially stimulated forest net primary productivity (NPP) by 24%. However, within a decade, N limitation attenuated this effect and NPP was similar to that measured under ambient CO_2 levels. Drought stress can also attenuate, or reverse, increased NPP that might be expected with CC (Ciais and others 2005; Wu and others 2011) due to increases in tree mortality (van Mantgem and others 2009; Clifford and others 2011). Finally, paleoecological studies in parts of western North America have shown that previous extended droughts correlated with greater extents of shrub-grassland species (Huerta and others 2009; Nelson and Pierce 2010; Whitlock and others 2011).

Modern CC may lead to similar patterns, as it has been implicated in large-scale tree mortality, shifts in forest composition (Iverson and Prasad 2002; Allen and others 2010; Bentz and others 2010), and reduced tree basal area in western North America (Rood and others 2008; van Mantgem and others 2009). More frequent insect outbreaks linked to CC moved ecotones up to 2 km in a 5-year period in southwestern North America (Allen and Breshears 1998), decreased canopy cover by 55% in a 2-year period, and eliminated increases in forest cover that had occurred since the 1930s (Clifford and others

2011). Even if forests currently show no signs of change, future shifts could occur rapidly. Trees can exhibit lagged population responses to ecological change so that forests persist for a time period despite conditions that reduce, or eliminate, seedling recruitment (Brubaker 1986; Turner 2010). In fact, forest cover can be committed to a 50% decline before any signs of impending dieback are detected (Jones and others 2009). Because modern CC may lead to conditions similar to past severe droughts of the Holocene (Cook and others 2004), the extent of shrub-steppe at low elevations in western North America is expected to increase with CC (Figure 1).

Greater fire activity may accelerate forest conversion, as it can trigger rapid conversion of stressed ecosystems (Turner 2010). Under past climate regimes, mixed conifer forests in western North America typically matured to pre-fire conditions in 100–200 years (Oliver 1981; Arno and others 1985), but the return interval for a stand-replacing fire was 200–400 years (Meyer and others 1992; Svenson 2010). This allowed old-growth forests to regenerate post-fire. However, forests may not reestablish and instead shift to a new ecosystem type if regeneration rates slow or fire return intervals shorten (Westerling and others 2011). This potential may increase because many trees at low elevations in western North America germinated during the cooler, wetter 'Little Ice Age' (1700–1900 AD; Grove 1988; Nelson and Pierce 2010). Indeed, during recent decades post-fire seedling recruitment has been negligible at low elevations in Idaho's Salmon River basin (Nelson and Pierce 2010), findings that echo the CC-induced 'savannification' of prairie-forest boundaries (Frelich and Reich 2010). Thus, there is mounting evidence that CC may decrease forest cover, increase the extent of shrub-grassland, and alter the dominant ecosystem type in many river basins of western North America.

EFFECTS OF CLIMATE CHANGE VIA LAND–WATER LINKAGES

Because streams rely on material and energy flows from terrestrial ecosystems (Minshall and others 1992; Webster and Meyer 1997), we next assessed how stream flow, temperature, light flux, and inputs of nutrients, sediment, and organic matter may be affected by changes in terrestrial processes (Figure 1). Our synthesis was based on extensive evidence examining stream responses to wildfire and changes in vegetation structure, but there are few studies assessing stream responses to beetle

outbreaks. We reasoned that beetle outbreaks may lead to similar patterns in tree mortality observed with stand-replacing fires and subsequently many similar consequences for streams. This remains to be corroborated by future investigations.

Hydrologic Inputs

Although CC may not affect total precipitation in western North America, it is expected to increase the proportion arriving as rain and the prevalence of rain-on-snow events. This may increase winter stream flows and reduce summer flows (Stewart 2009). Expected changes in terrestrial processes may further alter stream flow because run-off is a function of precipitation, soil composition, and vegetation cover that can differ in evapotranspiration rates (Huxman and others 2005; Adams and others 2012). For instance, a global meta-analysis showed that, on average, afforestation of shrub-grasslands can reduce annual stream flow by 31–44% (Farley and others 2005). Similar magnitude increases may occur when forests are converted to shrublands, changes that have been predicted in snowmelt-dominated regions when loss of forest cover reduces evapotranspiration (Adams and others 2012). Reduced evapotranspiration, earlier snowmelt, and increased stream flow have also been reported after large-scale wildfires and insect outbreaks (Gresswell 1999; Adams and others 2012; Pugh and Gordon in press). Thus, evidence suggests that CC-induced changes in terrestrial ecosystems may exacerbate effects of altered precipitation regimes on stream hydrology, but further study is needed to anticipate such potential interactions.

Stream Temperature

Higher air temperatures have warmed streams by 0.009–0.077°C per year in many regions (Kaushal and others 2010). However, wildfire can also warm streams as it reduces canopy cover and thermal insulation (Gresswell 1999). A study in western North America showed that thermal responses of streams to higher air temperatures were 2–3 times greater for burned versus unburned streams, likely due to reduced canopy cover (Isaak and others 2010). As there is evidence that insect outbreaks can lead to comparable canopy loss throughout western North America (Bentz and others 2010; Williams and others 2010), we speculate that increased pine beetle activity may similarly warm streams. Streams that experienced wildfire and a subsequent debris flow also had average maximum temperatures that were 8°C higher than unburned

streams and 4°C higher than burned streams (Dunham and others 2007). Under past climates that promoted regeneration of forest canopy after disturbances, such temperature increases have been short in duration (Minshall and others 1989). However, if CC reduces forest regeneration and shifts landscapes to shrub-steppe, post-disturbance warming may be prolonged. Thus, altered terrestrial processes may reinforce stream responses to higher air temperatures, warming streams more than would be expected based on air temperature increases alone. These effects should then be incorporated into future studies and modeling efforts aimed at generating quantitative estimates of stream temperature change.

Light Flux

Greater light flux can warm streams, but few studies have explicitly assessed effects of CC on light regimes. However, there is evidence that CC may increase light flux to forested streams, which could have effects that extend beyond warming (increased light can stimulate primary production). Severe wildfire can reduce canopy cover and increase light flux to the stream surface (Gresswell 1999; Romme and others 2011). However, light flux typically peaks soon after wildfire because of the regeneration of riparian vegetation (Romme and others 2011). Due to comparable loss of canopy cover, we expect that light flux responses would be similar after beetle outbreaks. In contrast to past climate regimes under which canopy cover quickly regrew, light flux in watersheds experiencing reduced or no forest regeneration might remain elevated. Thus, changes in terrestrial processes in western North America that reduce forest cover would increase light flux, effects that would not be expected based solely on shifts in temperature and precipitation.

Nutrient Inputs

Reductions in snow depth and thermal insulation can increase the duration and depth of soil freezing (Brooks and Williams 1999; Groffman and others 2011). This can increase soil leaching and nutrient inputs to streams (Brooks and Williams 1999; Fitzhugh and others 2001), but not in all cases. Groffman and others (2011) found that freezing had less effect on nutrient leaching when availability of dissolved organic carbon (DOC) was high, as this presumably increased nutrient sequestration by microbes. Conversely, a biogeochemical model predicted that alteration of thermal and precipitation regimes could increase soil leaching and stream nutrient export in deciduous forests by 2100

(Campbell and others 2009). Overall, evidence points to altered nutrient inputs due to changes in precipitation and temperature and the need for further research of such effects.

Evidence suggests that stream nutrient inputs can be affected similarly by altered terrestrial processes. Nutrient inputs to streams can increase immediately post-fire (Spencer and others 2003; Stephan and others 2012). However, soil nutrient retention increases as forests regrow (Vitousek and Reiners 1975) and inputs ultimately return to pre-fire levels (Spencer and others 2003; Romme and others 2011). This pattern may be mirrored during regeneration after beetle outbreaks. Even if tree regrowth declines and shifts forests to shrub-steppe, it may not affect long-term nutrient inputs. Invasion of grasslands by woody plants had little impact on soil nutrient availability due to faster microbial and nutrient turnover in grasslands (Booth and others 2005; McKinley and others 2008) that may reduce nutrient inputs. However, Berthrong and others (2009) showed that afforestation of shrub-grasslands can reduce soil nutrient content. Freezing effects on leaching also differed between forest type (Groffman and others 2011), suggesting that vegetation type may influence responses. Thus, soil freezing associated with thermal and precipitation shifts may increase nutrient inputs, but more research is needed to assess how changes in terrestrial processes will affect such inputs.

Sediment Inputs

Sediment inputs to streams are related to precipitation (Langbein and Schumm 1958), and therefore may be altered by CC-induced shifts in precipitation. For instance, sediment inputs can increase due to more frequent rain-on-snow events that increase winter floods, and inputs are predicted to further increase with CC-induced changes in terrestrial disturbance regimes (Goode and others 2012). Fire, in particular, can increase sediment inputs and reduce instream sediment storage, principally owing to fire-related debris flows (Cannon 2001; Wondzell and King 2003). Paleoecological data have also shown that variability of erosion rates during the Holocene (ca. last 10^4 years) is linked to climate and fire (Kirchner and others 2001; Pierce and others 2004). Severe drought during the 'Medieval Climatic Anomaly' (950–1250 AD) produced debris flows throughout the Rocky Mountains (Meyer and others 1992; Nelson and Pierce 2010). Conversely, because instream wood can increase sediment storage, forest regrowth after disturbance can reduce inputs and

increase storage (May and Gresswell 2003). Despite such regrowth, impacts on sediment dynamics are detectable up to 150 years post-debris flow (May and Gresswell 2003). Thus, even when forests regenerate, greater fire and debris-flow activity may increase sediment inputs, yet decrease storage.

Post-disturbance recovery of sediment inputs and storage can be a function of forest regrowth; thus, conversion to shrub-steppe may magnify sediment responses to shifts in precipitation regimes. Sediment inputs to streams are a function of forces that resist erosion (rooting depth and soil cohesion) and forces that facilitate sediment movement (slope and soil saturation). On forested slopes, greater soil cohesion from tree roots and soil moisture can reduce sediment inputs (Schmidt and others 2001). For instance, throughout the Holocene, shrub-steppe had higher baseline sediment inputs due to reduced rooting depth, increased raindrop impact, and less water infiltration that increased run-off. Rather than rarer large magnitude failures on forested slopes, shrub-dominated slopes experienced frequent, but lower magnitude, sheetfloods (floods that deposit sediment when channels become unconfined; Pierce and others 2004; K. Riley and J. Pierce unpubl. data). In fact, sediment inputs to streams have been projected to increase 10 times in parts of western North America due to changing precipitation regimes, wildfire and debris-flow activity, and vegetation structure (Goode and others 2012). Sediment retention in stream channels may also decline due to reduced forest regrowth that reduces wood inputs to streams. This suggests that CC-induced changes in terrestrial processes will likely magnify increases in sediment inputs and decreases in sediment storage projected based on precipitation alone.

Organic Matter Inputs

Altered precipitation and thermal regimes may affect inputs of organic matter (leaf litter, DOC, and wood) to streams, but changes will largely result from terrestrial processes (plant productivity, drought, and disturbances). For instance, higher air temperatures can increase terrestrial plant production (Wu and others 2011), which may increase availability and inputs of organic matter. Drought stress, however, can increase tree mortality (van Mantgem and others 2009; Clifford and others 2011) and attenuate greater plant production (Ciais and others 2005; Wu and others 2011). Under scenarios in which forests regenerate and do not shift toward shrub-steppe, inputs may still increase if plant biomass turns over faster. Reduced snowpack

can also increase DOC leaching from soils (Groffman and others 2011), but others have found no such response (Hentschel and others 2009). However, due to the importance of terrestrial detritus as an instream DOC source (Meyer and others 1998), DOC inputs may increase as inputs of wood and detritus increase.

Although organic matter inputs may increase under scenarios in which forests regrow post-disturbance, considerable evidence suggests that parts of western North America will experience reductions in forest cover (Rood and others 2008; Allen and others 2010; Bentz and others 2010). Additionally, paleoecological studies show a greater spatial extent of shrub-steppe in western North America during previous droughts (Huerta and others 2009; Nelson and Pierce 2010; Whitlock and others 2011). This suggests a more likely scenario will be reductions in forest cover that decrease organic matter inputs. Due to reduced canopy cover, non-forested streams have lower inputs and standing crop of organic matter than forested streams (Webster and Meyer 1997). Inputs to a shrub-grassland stream in southeastern Idaho were orders of magnitude lower than to a coniferous-forested stream in central Idaho (2.4 vs. 339.9 g AFDM $m^{-2} y^{-1}$) (Minshall and others 1992; Webster and Meyer 1997). Consequently, organic matter inputs would be predicted to decrease when forest regeneration and cover decline, a likely scenario throughout western North America.

Altered terrestrial processes may affect wood inputs, which retain organic matter and maintain habitat in streams (Megahan 1982; Gurnell and others 2002). Wildfire can increase short-term inputs, as snags from both streamside and hillslopes are recruited into stream channels (Gresswell 1999; Benda and others 2003). Long-term inputs return to pre-fire levels as the pool of snags is depleted and trees regrow, patterns likely to occur after large-scale tree mortality due to beetle outbreaks. Conversely, debris flows can reduce the amount of wood in low to mid-order stream channels by removing riparian vegetation, such that the dominant habitat can be bedrock even 100 years post-debris flow (May and Gresswell 2003). Despite short-term effects of terrestrial disturbances, long-term wood inputs and standing crop recovered to pre-disturbance levels as forests regenerated under past climate regimes, a process that could take more than 100 years (Minshall and others 1989; Jones and Daniels 2008). However, if reductions in forest regeneration and conversion to a shrub-steppe occur, this might reduce wood inputs and standing crop. Shrubs can contribute woody debris and

experience more frequent fires (fire return interval of 70–200 years; Baker 2006), but their smaller twigs and branches are unlikely to be functional substitutes for trees. Thus, greater disturbance activity and reduced forest regeneration may override greater wood inputs predicted with CC-induced increases in drought and terrestrial productivity. Persistent reductions in inputs may ultimately reduce wood standing crop in stream channels and decrease organic matter retention. Such results would not be predicted without incorporating terrestrial processes into predictive frameworks.

Autotrophic Production

Because production of photoautotrophs is related to many factors (flow, light, nutrients, and sediment; Biggs 1996) that may change via terrestrial processes, it may exhibit complex responses to CC. Stream warming may stimulate autotrophic production as it is positively related to temperature (Mulholland and others 2001; Yvon-Durocher and others 2010). Flow effects may vary seasonally as high flows, in general, reduce primary production and low flows increase it (Uehlinger and Naegeli 1998; Marcarelli and others 2010). A shift to a rain-dominated hydrology that increases frequency of winter floods may decrease productivity in the winter, whereas it may increase in the summer due to lower baseflow. Compared to the summer, post-flood recovery can also be slower in the winter when temperature and light flux are lower (Uehlinger and Naegeli 1998). Thus, annual production may decrease if declines in winter production are sustained over longer periods and are larger than increases in the summer.

Shifts in terrestrial processes will likely mediate responses of primary production to CC. As photoautotrophs can be light limited (Mulholland and others 2001; Kiffney and others 2003), shifts in terrestrial disturbances that reduce canopy cover may increase primary production. Few studies have assessed effects of fire on primary production in temperate streams, but primary production increased post-fire in boreal forest streams (Betts and Jones 2009). Algal biomass was also higher in burned versus unburned forested streams in Idaho (Minshall and others 2001). Although primary productivity was higher post-debris flow, biomass (AFDM) was lower and responses returned to pre-disturbance levels as forests regenerated (Cover and others 2010). We expect that primary production may respond similarly to beetle outbreaks due to comparable trends in tree mortality and regrowth.

Given the importance of tree regeneration for recovery of stream production, reduced forest regrowth may sustain higher production over longer periods. Conversely, changes may reduce primary production. Turbidity and light attenuation to the benthos can reduce primary production (Young and Huryn 1996). Sediment can similarly increase abrasion and reduce algal biomass (Biggs 1996). In Yellowstone National Park, sedimentation was thought to be a primary reason that short-term increases in algal biomass did not persist with post-fire increases in light flux (Romme and others 2011). This suggests increased sediment inputs related to terrestrial disturbances could decrease production by reducing light flux to the benthos and increasing abrasion.

The net response of autotrophic production will depend on the relative magnitude of positive (light) and negative (sediment) effects. Productivity may increase if light flux to the stream surface is more important, but decrease if turbidity is more important. Despite such uncertainty, an inter-biome comparison found that light, nutrients, and temperature explained 90% of variation in gross primary production and light alone explained 53% of variation in net ecosystem production (Mulholland and others 2001). In that study, the only stream that was strongly autotrophic was an open canopy stream that drained arid grassland and experienced frequent floods. Kiffney and others (2003) also showed that reductions in canopy cover can increase autotroph biomass, even with stream warming of 4°C. Furthermore, evidence indicates that a CC-induced shift from a snow- to rain-dominated hydrology may increase autotroph biomass in the summer (Davis and others 2013). These studies suggest that autotrophic production will increase with a combination of changing precipitation, temperature, and terrestrial–aquatic linkages, leading to increases that are larger than those expected based on thermal and flow effects alone. However, new studies are needed that more fully evaluate these potential interactive effects on autotrophic production.

Consequences for Stream Animals and Ecosystem Processes

Stream metabolism and secondary production are a function of autotrophic production; thus, its alteration would likely cascade throughout stream food webs. Indeed, evidence from outside the realm of CC research has shown, in general, that many stream animals are sensitive to changes in terrestrial processes (Gresswell 1999; Dunham and

others 2007), which may subsequently alter their response to CC-induced changes in flow and temperature. For example, if wildfire or insect outbreaks result in more light input to streams, this may not only increase primary production but also invertebrate secondary production, as has been demonstrated via comparisons of stream reaches with open versus closed canopy (Behmer and Hawkins 1986). Similarly, disturbances like wildfire can cause shifts in stream communities to greater biomass and dominance of disturbance-adapted macroinvertebrate taxa (Romme and others 2011). This may also contribute to increased secondary production and emergence of adult aquatic insects (Malison and Baxter 2010). Fire can also alter energy flow through food webs, increasing reliance on autochthonous resources (Spencer and others 2003), reducing populations of taxa that specialize on terrestrial detritus, and increasing populations of trophic generalists (Minshall and others 2001). Likewise, ecosystem processes can be influenced by terrestrial disturbances and riparian vegetation state (Campbell and others 2009; Cover and others 2010). For instance, fire can increase ecosystem respiration (ER) as well as gross primary productivity, and affect stream carbon and nutrient dynamics (Betts and Jones 2009). Conversely, ER could decrease because it is linked to organic matter standing crop (Roberts and Mulholland 2007), which may be diminished with reduced input of terrestrial detritus. Thus, CC may affect streams via these pathways, but predicting such responses entails large uncertainty because few studies have focused on these impacts. Accuracy is further constrained by limited understanding of CC effects on primary production discussed above. Despite such uncertainty, it is likely that predicting responses of stream food webs and ecosystem processes to CC will require incorporation of shifting terrestrial disturbance regimes and attendant changes in land–water linkages.

CONCLUSION

Our synthesis provides evidence that in regions where CC is altering terrestrial disturbance regimes and shifting ecosystem distributions, its effects on streams will not be limited to changes in flow and temperature. For instance, we synthesized evidence showing how CC-induced alterations of terrestrial ecosystem structure and disturbances like wildfire and insect outbreaks may affect land–water linkages. This identified additional pathways by which CC may affect streams in western North America and similar ecosystems elsewhere

(increased light flux, decreased organic matter inputs, and increased sediment inputs). Because such changes will presumably alter the ecological context within which precipitation and thermal shifts are occurring, this suggests the need for a framework that incorporates changes in terrestrial processes when anticipating stream responses to CC. It may be challenging to integrate this added complexity into predictive models. However, their exclusion poses even greater problems because of the growing evidence that CC is altering many terrestrial processes that affect streams. Thus, similar to the way that incorporation of disturbance regimes and vegetation changes informs predictions about warming and the global carbon cycle (Goetz and others 2007; Kurz and others 2008), their integration may improve understanding of how streams will respond to CC. Our synthesis represents only the first step in this understanding and highlights the need for more study.

This synthesis focused on river basins of western North America to examine how the effects of CC might be better anticipated by integrating CC-induced alteration of terrestrial processes. Thus, it is most relevant to mountainous river basins that are expected to shift from snowmelt- to rainfall-driven hydrology, experience increases in activity of natural disturbances (wildfire, debris flows, insect outbreaks), and shift from forests toward shrub-grassland. However, CC is expected to drive similar changes in other biomes (Barnett and others 2005; Bentz and others 2010; Gonzalez and others 2010; Moritz and others 2012); therefore, this synthesis may be applicable to those ecosystems as well. For instance, large-scale tree mortality related to drought and insect outbreaks has been observed outside of western North America (Allen and others 2010) and could eventually lead to a savannification of some grassland–forest boundaries (Frelich and Reich 2010). Thus, some of the potential effects we have identified (increased light flux that stimulates autotrophic production) may be expected to occur beyond western North America. In ecosystems that are not experiencing the same terrestrial ecosystem changes, we would expect responses to deviate from those presented here. However, even in these regions, a framework that incorporates land–water linkages may help anticipate broader CC effects.

Evidence from deciduous-dominated forests suggests streams there may also be affected by CC-induced alterations of terrestrial processes. For instance, a key pathway by which CC may alter streams in western North America is via decreases in canopy cover associated with forest conversion to shrub-steppe. In other regions, deciduous forests may not be reduced, but rather are predicted to dramatically change in their composition via at least 50% declines in the ranges of some tree species and increases of similar magnitude for other species by 2100 (Iverson and Prasad 2002). In addition, interactions between nonnative plants and warming are facilitating the conversion of deciduous forests to evergreen forests in Europe (Walther 2004). In such regions, CC may alter the composition of watersheds without decreasing overall forest cover. Due to differences in detritus quality, evapotranspiration, and biogeochemical cycling, changes in composition of deciduous forests can have bottom-up effects on streams (Ball and others 2010; Kominoski and Rosemond 2011). Such effects would not be predicted based on thermal and flow regime shifts alone.

Effects of CC will likely extend beyond thermal and flow regime shifts in tundra and boreal ecosystems as well. For example, CC is increasing tree cover in tundra ecosystems (Gonzalez and others 2010) and is expected to shift some boreal forests from conifer to deciduous-dominated ecosystems (Gonzalez and others 2010; Wolken and others 2011) while rapidly converting others to shrub-steppe (Scheffer and others 2012). Similar to our focal region, such shifts are linked to increased fire activity, insect outbreaks, and permafrost thawing (Wolken and others 2011), changes expected to continue with CC (Wolken and others 2011; Moritz and others 2012). By 2100, fire activity is predicted to increase on 90% of land area currently covered by boreal forest and tundra (Moritz and others 2012), and in turn may alter canopy cover and detritus inputs to streams. Stream productivity may also be more directly affected by changes in terrestrial inputs due to wildfire (Betts and Jones 2009) and permafrost thawing (Bowden and others 2008). Although responses may differ from those expected in mountain streams, integrating CC-induced alteration of terrestrial processes will still be needed to predict pathways of change in tundra and boreal streams (Ball and others 2010).

We focused on terrestrial processes that are expected to be altered by CC in western North America, but additional processes may lead to complex interactions with CC in other regions. Human activities and CC may facilitate the spread of some nonnative species (Walther 2004). For example, the range of introduced Japanese knotweed (*Fallopia japonica*) in Europe may expand due to warming (Beerling 1993) and affect streams (Lecerf and others 2007). In addition, anthropogenic nutrient enrichment can directly impact

stream productivity and carbon dynamics (Dodds 2007), and exacerbate stream responses to CC (Moss 2010). It can also modify relationships between CO_2 fertilization and terrestrial NPP (Norby and others 2010), which may in turn alter biogeochemical cycling (Campbell and others 2009). Thus, stream responses to CC cannot be fully understood in isolation of these additional ecological changes because they can affect similar pathways as those influenced by CC. Here, we have taken initial steps toward improved anticipation of stream responses to CC by incorporating effects via land–water linkages. We expect that addressing additional layers of complexity will be needed to improve the reliability of predictions, but we hope that this process will be facilitated by the conceptual framework we have presented here.

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