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# Anticipating Stream Ecosystem Responses to Climate Change: Toward Predictions That Incorporate Effects via Land–Water Linkages

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# Forecasting stream ecosystem responses to climate change: toward predictions that incorporate indirect effects via land-water linkages

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JMD, CVB, EJRM, JLP, and BTC conceived the research question and developed the ecosystem model. JMD and CVB wrote the manuscript with contributions from EJRM, JLP, and BTC.

## Abstract

Climate change (CC) is predicted to increase the frequency and severity of natural disturbances and shift distributions of terrestrial ecosystems. Western North America, in particular, is predicted to experience CC-induced alteration of forest boundaries due to changes in wildfire, debris flows, and insect outbreaks. Because stream ecosystems are coupled to terrestrial ecosystems via flows of material and energy, such shifts in terrestrial disturbance regimes and ecosystem distributions will likely affect stream ecosystems. However, predictions of stream responses to CC have not incorporated these potentially important effects of altered terrestrial processes. Here, we use a conceptual ecosystem model to assess how responses of forested stream ecosystems to CC will be related to not only direct effects of thermal and hydrologic shifts, but also indirect effects of altered terrestrial processes (i.e., disturbance regimes and vegetation structure). Because effects of terrestrial processes on streams have been well-studied in contexts largely independent of CC research, we synthesize and apply this knowledge to generate predictions of how CC-induced alterations of terrestrial ecosystems may change stream ecosystem structure and function. Our analysis indicates that altered terrestrial processes will change terrestrial inputs, biotic production, and carbon dynamics, yielding greater climate sensitivity than would be expected based solely on shifts in temperature and precipitation regime. It also indentified uncertainties that presently constrain predictions of some responses, such as ecosystem metabolism and carbon export. Therefore, accurate prediction of CC effects on temperate stream ecosystems may be strongly coupled to the accuracy of predictions for long-term changes in terrestrial processes.

Keywords: *climate change, wildfire, disturbance regime, stream food web, qualitative model*

Understanding the ecological consequences of climate change (CC) will require approaches that encompass possible feedbacks and interactions, as they may influence the magnitude and direction of the overall effects of CC. For example, when responses of vegetation and disturbance regimes to CC are not integrated into predictive models, models may under- or overestimate projected air temperature increases due to CC (Goetz and others 2007; Kurz and others 2008). Wildfires that convert coniferous forests to grasslands or deciduous forests may increase albedo and negative feedbacks to CC (Goetz and others 2007). Conversely, vegetation changes due to insect outbreaks or wildfire can reduce carbon storage, providing positive feedbacks to CC (Goetz and others 2007; Kurz and others 2008). A range of terrestrial, freshwater, and marine ecosystems will be sensitive to warming (Rosenzweig and others 2008), but such interactions that amplify or dampen expected temperature shifts will pose a challenge to accurate predictions of these ecosystem sensitivities.

Stream ecosystems likely will be affected directly by CC, but other ecological factors may alter these responses of streams. In terms of direct effects, many stream organisms are ectothermic and can be sensitive to thermal change (Thackeray and others 2010) and have adapted to past flow regimes that will likely shift with CC (Poff and others 2010; Woodward and others 2010). Because research largely has focused on assessing 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), and interactions (Woodward and others 2010). However, CC is occurring coincidently with other ecological changes (e.g., land-use change and nutrient enrichment) that are known to affect streams and may magnify or attenuate stream responses to CC (Kaushal and others 2010; Moss 2010). For instance, simultaneous nutrient enrichment and higher water temperatures led to severe deoxygenation and increased fish mortality beyond what was expected based on these changes alone (Moss 2010). Similarly, stream acidification negated thermal effects, such that stream warming over a 25-yr period reduced invertebrate abundance in reference streams, but not in acidified streams (Durance and Ormerod 2007). Thus, predicted effects of CC could be over- or underestimated if the ecological context in which changes are occurring is not considered.

Overall responses of stream ecosystems to CC may be underestimated if predictions do not take into account the consequences of shifts in forest ecotones and terrestrial disturbance regimes, such as the 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). Because terrestrial and stream ecosystems are linked via inputs of nutrients, sediment, organic matter, and light flux, changes to terrestrial ecosystems can affect streams (Likens and Bormann 1974; Hynes 1975) and even small alterations of forest composition may affect stream responses to global change (Ball and others 2010). As natural disturbances can have dramatically larger effects on terrestrial ecosystems and inputs, alterations of disturbance regimes by CC will likely change streams. For instance, wildfire and fire-related debris flows (i.e., liquefied landslides that scour stream channels) can remove canopy cover, increasing light flux and stream temperatures and affecting stream biota (Dunham and others 2007; Romme and others 2011). Also, greater disturbance activity due to CC may not just alter species ranges and forest assemblages, but will likely move ecosystem boundaries and convert forests to shrub-grasslands in regions worldwide (Shafer and others 2001; Williams and others 2007; Frelich and Reich 2010). Between 10-50% 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, CC-induced alteration of terrestrial processes (i.e., disturbance regimes and ecosystem distributions) will likely change the context of CC and our ability to predict stream responses.

At present there are few CC studies upon which to develop predictions that integrate both direct and indirect effects of CC on streams, but that does not mean the scientific community has no basis for generating such predictions. There is a rich history of research that has been dedicated to understanding ecological linkages between streams and their watersheds (e.g., Likens and Bormann

1974; Hynes 1975; Ball and others 2010), and the principals that have emerged should be brought to bear on this challenge. Effects of altered terrestrial processes on streams have been well-studied, albeit in contexts largely independent of CC (e.g., wildfire and deforestation; Gresswell 1999; Kiffney and others 2004; Romme and others 2011). Their importance has also begun to be assessed 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 in this region largely has focused on effects of changing temperature and flow without explicitly integrating impacts of altered terrestrial processes. However, by leveraging knowledge of how terrestrial processes, in general, can affect streams, we can begin to predict how similar CC-induced shifts in such processes may alter stream structure and function.

*Research objectives:* Here, we evaluate whether predicting long-term effects of CC on forested temperate streams requires an approach that not only encompasses the direct effects of thermal and flow regime shifts, but also integrates indirect effects associated with altered terrestrial disturbance regimes (e.g., drought, wildfires, beetle outbreaks, and debris flows) and ecosystem distributions (Fig. 1). We addressed this question in the context of mountainous river basins of western North America, a region where stream responses to terrestrial disturbances and the direct effects of CC have been well-studied. First, by reviewing current evidence, we show that 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 it is comparable to historic fire return intervals (200-400 yrs) and time required for mixed conifer forests to reach old-growth status (200-500 yrs; Oliver 1981; Arno and others 1985; Nelson and Pierce 2010). Although effects of these changes may differ over shorter periods, focusing on longer periods allowed assessment of effects once forests have converted to a new ecosystem type. Next, we show that greater disturbance activity is predicted to alter ecosystem distributions and shift the dominant ecosystem types drained by river networks (Appendix 1), alterations that will likely have consequences for streams.

Using the extensive literature that evaluates how terrestrial processes can affect streams via changes in temperature and inputs of sediment, nutrients, and organic matter, we develop a conceptual ecosystem model that assessed how similar CC-induced shifts in terrestrial disturbances and ecosystem distributions could affect terrestrial inputs (Fig. 2). Based on the model, we predicted how changes in such inputs could affect stream temperature, organic matter standing crop, substrate stability, and consequences for stream biota and carbon dynamics (Fig. 3). By contrasting predictions that integrated indirect effects of CC on streams (i.e., terrestrial processes) with those based only on thermal and precipitation regime shifts, we assessed if the net effect of CC may be under- or overestimated. Predictions are most relevant to mountainous river basins of western North America, but similar changes in hydrology, disturbance regimes, and ecosystem boundaries are expected worldwide (Barnett and others 2005; Flannigan and others 2009; Bentz and others 2010; Gonzalez and others 2010). Thus, our analysis was intended to broadly inform predictions of direct and indirect effects of CC across a range of regions and provide guidance for future research.

We used a qualitative approach, as first proposed by Levins (1966), to develop the conceptual ecosystem model and compare direct and indirect effects of CC on streams. Qualitative models can provide a framework for integrating across disciplines to assess responses of complex systems to perturbation, especially when magnitudes of some parameters are unknown (Justus 2005). This heuristic approach is a valuable first step in generating predictions, augmenting quantitative models that often focus on subsets of a system, and identifying uncertainties that will require future study.

## Effects on terrestrial processes

*Effects on 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, higher air temperatures have reduced snowpack as more precipitation occurs as rain (Knowles and others 2006); changes projected to increase the frequency of winter floods and decrease summer baseflow (Stewart 2009). Warming also has shifted spring snowmelt earlier and reduced the size of spring run-off in this region (Stewart 2009; Kunkel and Pierce 2010). From 1948-2002, snowmelt occurred 10-20 days earlier and will be even earlier by 2100 (Stewart and others 2004). Thus, CC may not affect total annual precipitation, but is expected to change when and how it falls, increasing the prevalence of winter floods and terrestrial disturbances due to transitions from snowpack accumulation to rain-on-snow events (Fig. 1).

*Effects on terrestrial disturbances:* Because air temperature and precipitation regulate wildfire activity (Gedalof and others 2005), reduced snowpack and earlier snowmelt have increased summer drought stress and the frequency and severity of wildfire (Westerling and others 2006) and fire-related debris flows (Pierce and others 2004). Wildfire area in western North America is expected to increase 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 ca. 2050 (Westerling and others 2011). Increased wildfire 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). In one study, 54% of streams that were affected by wildfire experienced a debris flow within 30 yrs of fire, in contrast to 12% of unburned streams, and effects were still detectable >100-yrs post-debris flow (May and Gresswell 2003). Paleoecological records have found similar correlations between climate, fire, and debris flows (Pierce and others 2004), indicating that current warming also may increase their frequency (Fig. 1).

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

*Effects on vegetation structure:* Changes in disturbance regimes will likely influence forest composition and regeneration (Shafer and others 2001; Williams and others 2007). For example, paleoecological studies in parts of western North America have shown that previous extended droughts correlated with greater extent of shrub-grassland species (Beiswenger 1991; 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 (Bentz and others 2010; Williams and others 2010), and reduced tree basal area and canopy cover in western North America (van Mantgem and others 2009; Clifford and others 2011). Reductions in seedling recruitment due to CC are projected to decrease the extent of floodplain forests in North America (Rood and others 2008). More frequent insect outbreaks linked to CC also moved ecotones up to 2 km over a 5 yr period in southwestern North America (Allen and Breshears 1998), decreased canopy cover by 55% in a 2 yr period, and eliminated increases in forest cover that occurred since the 1930s (Clifford and others 2011). Even when forests currently exhibit no signs of change, future shifts may still occur rapidly. For instance, trees can be long-lived and have lagged population responses to ecological change; thus, forests may persist despite ecological changes 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). As greater drought sensitivity of low elevation forests can move ecotones upslope (Knutson and Pyke 2008) and 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 is likely to increase in the future (Fig. 1; Appendix 1).

Increased wildfire activity may accelerate forest conversion as it can rapidly convert stressed ecosystems to new ecosystem types (Turner 2010). Under past climate regimes, mixed conifer forests in western North America typically matured to pre-fire conditions in 100-200 yrs (Oliver 1981; Arno and others 1985), but the return interval for a stand-replacing fire was even longer (200-400 yrs; Minshall and others 1989; Meyer and others 1992; Svenson 2010). This allowed old-growth forests to regenerate after wildfires. However, forests may not reestablish post-fire and may shift to a new ecosystem type if regeneration rates slow or fire return intervals shorten (Westerling and others 2011). This potential may increase as many trees at low elevations in western North America germinated during a cooler, wetter interval known as the 'Little Ice Age' (1700-1900 AD; Grove 1988; Nelson and Pierce 2010). Preliminary evidence also suggests negligible post-fire seedling recruitment 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). If trends persist or accelerate, it could convert entire ecosystems, shift forests upslope, and alter the dominant ecosystem type in many river basins of western North America (Fig. 1).

### Effects on resource flows to streams

Because streams rely on material and energy flows from terrestrial ecosystems (Minshall and others 1992; Webster and Meyer 1997), we now evaluate how altered terrestrial processes may affect stream temperature, light flux, and inputs of nutrients, sediment, and organic matter (Figs. 1 and 2); integrate direct and indirect effects into our ecosystem model (Fig. 3); and compare net effects on stream structure and function (Tables 1-3). Our analysis was based on considerable evidence examining stream responses to wildfire and changes in vegetation structure, but there are few studies assessing stream responses to beetle outbreaks. We reason that beetle outbreaks may lead to similar patterns in tree mortality observed with stand-replacing fires and subsequently many similar consequences for streams, though this remains to be corroborated by future investigations.

*Stream temperature:* Higher air temperatures have warmed streams by 0.009 – 0.077 °C per year in many ecoregions (Kaushal and others 2010). However, wildfire can also warm streams as it reduces canopy cover and thermal insulation (Royer and Minshall 1997; Gresswell 1999). A study in western North America showed that thermal responses of streams to higher air temperatures were 2-3× greater for burned vs. unburned streams (Isaak and others 2010). As there is considerable evidence that outbreaks can lead to comparable tree mortality and 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 8º C higher than unburned streams (23.5 vs. 15.6ºC) and 4ºC higher than burned streams (23.5 vs. 19ºC; Dunham and others 2007). Under past climates that promoted regeneration of forest canopy, elevated post-disturbance temperatures were short in duration (Minshall and others 1989). However, if CC reduces forest regeneration and shifts landscapes to shrub-steppe, post-disturbance thermal effects may be prolonged (Table 1; Fig. 3). Thus, altered terrestrial processes may reinforce stream responses to higher air temperatures, warming streams more than would be expected based on direct effects alone.

*Light flux:* Greater light flux can increase stream temperatures, but few studies have explicitly assessed effects of CC on light regimes. However, there is ample evidence that CC may increase light flux to forested streams, which could have effects that extend beyond temperature increases (i.e., 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). Five years post-fire, light flux to streams that experienced severe wildfire was 2× greater than to unburned streams (Malison and Baxter 2010), but light flux typically peaks soon after wildfire because of rapid regeneration of riparian vegetation (Fig. 2; Romme and others 2011). Due to comparable loss of canopy cover, we expect that temporal patterns of light flux responses would be similar after beetle outbreaks. In contrast to past climate regimes where canopy cover quickly regenerated, light flux in watersheds experiencing reduced or no forest regeneration might remain elevated (Fig. 2). A consequence may be that effects of terrestrial disturbances on light regimes that were historically short-lived may become more chronic. Thus, terrestrial processes may increase light flux more than would be expected based solely on temperature and precipitation effects (Table 1; Figs 2 and 3).

*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 may increase soil leaching, and nitrogen and phosphorus inputs to streams (Brooks and Williams 1999; Fitzhugh and others 2001), but not in all cases (Groffman and others 2011). Nutrient leaching responses to freezing were lower with higher availability of dissolved organic carbon (DOC), likely due to greater microbial activity and nutrient sequestration (Groffman and others 2011). Leaching also differed with forest type (Fitzhugh and others 2001). Despite some contrasting results, evidence suggests the potential for temperature and precipitation regime shifts to increase nutrient inputs (Table 1).

Altered terrestrial processes may not change increases in nutrient inputs expected due to thermal and precipitation shifts. 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 can return to pre-fire levels over longer periods (Spencer and others 2003; Romme and others 2011), a pattern that may be mirrored during regeneration after beetle outbreaks. Even if forest regeneration declines and shifts them to shrub-steppe, it may not affect long-term nutrient inputs. Invasion of grasslands by woody plants had little effect on soil nutrient availability due to faster microbial and nutrient turnover in grasslands (Booth and others 2005; McKinley and others 2008). Rapid turnover would likely sequester leachates and reduce export. On the other hand, freezing effects on leaching differed between sugar maple and yellow birch forests (Groffman and others 2011), suggesting the potential for vegetation type to influence responses and the need for more studies. Thus, soil freezing may increase nutrient inputs, but there is currently little evidence that terrestrial processes will substantially affect inputs (Table 1; Fig. 3).

*Sediment inputs*: Altered disturbance regimes due to CC likely will affect sediment inputs. Over long timescales ($10^3$ to $10^4$ yr), extended drought can increase the frequency and magnitude of large sedimentation events. For instance, prolonged warming and drying during the 'Medieval Climatic Anomaly' (ca. 950–1250 AD) produced debris flows throughout the northern Rocky Mountains (Meyer and others 1992; Pierce and others 2004; Nelson and Pierce 2010). Erosion rates in central Idaho during the Holocene (ca. last $10^4$ yr) also have not been constant through time and have been related to climate (Kirchner and others 2001; Meyer and others 2001; Pierce and others 2004). As droughts induced by current CC may reach the severity of those accompanying earlier Holocene warming (Cook and others 2004), sediment inputs may increase in mountainous regions. Greater fire activity may further increase inputs. For example, considerable evidence shows that wildfires can increase sediment inputs and reduce instream sediment storage, particularly during fire-related debris flows (Cannon 2001; May and Gresswell 2003; Wondzell and King 2003). Because sediment storage increases linearly with instream wood (May and Gresswell 2003), forest regrowth after disturbance may reduce inputs and increase storage. However, effects have been detected up to 150 yrs post-debris flow (May and Gresswell 2003). Therefore, even when forests regenerate, greater wildfire and debris-flow activity may increase sediment inputs, yet decrease storage (Table 1; Figs. 2 and 3).

Given the importance of forest regeneration for the recovery of sediment dynamics, conversion to shrub-steppe likely would magnify sediment responses. Sediment inputs to streams are a function of forces that resist hillslope erosion (e.g., rooting depth and density, soil cohesion, and friction) and forces that facilitate sediment movement (e.g., slope and soil saturation). On forested slopes, greater soil cohesion from tree roots and soil moisture can reduce sediment inputs (Schmidt and others 2001). Shrub-steppe had higher baseline sediment inputs due to reduced rooting depth, combined with increased raindrop impact and less water infiltration. Shrub dominated slopes also exhibited more frequent, but lower magnitude, sheetflood events (i.e., sediment-rich floods that deposit sediment when channels become unconfined), rather than rarer large magnitude slope failures and debris flows on forested slopes (Pierce and others 2004; K. Riley and J. Pierce unpubl. data). Sediment retention also may decline due to reduced forest regrowth that reduces wood inputs to stream channels (see below). Thus, changes in terrestrial processes would be expected to sustain higher sediment inputs and reduced sediment storage for longer periods (Table 1; Figs. 2 and 3).

*Terrestrial organic matter inputs:* Although altered precipitation and thermal regimes may affect inputs of organic matter (i.e., leaf litter and DOC) and wood to streams, changes will result from greater terrestrial productivity and drought stress. 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 also increase tree mortality (van Mantgem and others 2009; Clifford and others 2011), which can attenuate, or reverse, greater plant production (Wu and others 2011). This greater mortality may still increase inputs if forests regenerate post-drought and plant biomass turns over faster. Evidence also suggests that reduced snowpack can increase DOC leaching in soils (Groffman and others 2011) and may increase inputs to streams, but others have found no DOC response (Hentschel and others 2009). However, leaching from instream organic matter can be an important DOC source (Meyer 1998); thus, DOC inputs may still increase as inputs of wood and detritus increase. If forests regenerate post-disturbance, CC-induced shifts in terrestrial processes would be expected to increase organic matter inputs (Table 1; Fig. 3).

Reduced forest regeneration and shifts to shrub-steppe would likely decrease inputs of organic matter. Because of greater canopy cover, forested streams have higher inputs and standing crop than non-forested streams (Webster and Meyer 1997). For instance, inputs to Camp Creek, a coniferous-forested stream in Idaho's Salmon River basin, are orders of magnitude higher than inputs to Deep Creek, a shrub-grassland stream in southeastern Idaho (339.9 vs. 2.4 g AFDM $m^{-2}$ $yr^{-1}$) (Minshall and others 1992; Webster and Meyer 1997). DOC inputs may similarly decline because of reductions in detritus inputs (e.g., Meyer 1998). Consequently, organic matter inputs would be predicted to decrease in scenarios when forest regeneration and cover decline (Table 1; Fig. 3).

Altered terrestrial processes will likely affect wood inputs, which can retain organic matter and maintain habitat in high gradient streams (Megahan 1982; Gurnell and others 2002). Wildfire can increase short-term inputs, as fire-killed snags from both streamside and hillslope sources are recruited (the latter via deposits from landslides and debris flows) into stream channels (Fig. 2; Benda and others 2003; Robinson and others 2005; Romme and others 2011). Long-term inputs return to pre-fire levels as the pool of snags is depleted and trees regenerate, 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 and sources of wood (May and Gresswell 2003; Cover and others 2010), such that the dominant habitat can be bedrock even a 100 yrs 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 a century (Minshall and others 1989; Jones and Daniels 2008). Reduced regeneration and conversion to a shrub-steppe may slow this recovery, reducing inputs and standing crop (Fig. 2). Shrubs can contribute woody debris and experience more frequent wildfires (fire return interval of 70-200 years; Baker 2006), but their smaller stature indicates that alternate wood sources (i.e., twigs and small branches) may be inadequate substitutes for trees. Moreover, expected replacement of woody plants by annual invasive grasses (e.g., cheatgrass: *Bromus tectorum*) following fire (Billings 1994) may further reduce fire return intervals and wood inputs. Thus, greater disturbance activity and reduced forest regeneration may override greater wood inputs predicted with CC-induced increases in drought and terrestrial productivity (Table 1; Figs. 2 and 3). Persistent reductions in inputs may ultimately reduce wood standing crop in stream channels and decrease organic matter retention, results that would not be predicted without incorporating terrestrial processes into predictive frameworks.

### Effects on instream structure and function

*Autotrophic production:* Autotrophs may exhibit complex responses to CC as their production is related to various factors (e.g., flow, nutrients, light, and substrate stability; Larned 2010) that will likely change. Higher stream temperatures may increase autotrophic production as it is positively related to temperature (Fig. 3; Mulholland and others 2001; Yvon-Durocher and others 2010). Flow effects may vary seasonally as high flows, in general, decrease 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 baseflow reductions. Post-flood recovery of production also can vary seasonally, such that recovery is slower in the winter when temperature and light flux are lower (Uehlinger 2000). Annual production may decrease if declines in winter production are sustained over longer periods and are larger than increases in the summer (Table 2; Fig. 3).

Shifts in terrestrial processes will likely affect stream autotrophs. As photo-autotrophs can be light limited (Mulholland and others 2001; Kiffney and others 2004), terrestrial disturbances and shifts in vegetation structure that reduce canopy cover over streams may increase primary production (Fig. 3). There are few data assessing effects of wildfire on primary production in temperate streams, but it increased post-fire in boreal forest streams (Betts and Jones 2009). Algal biomass was also higher in burned vs. unburned forested streams in Idaho (Minshall and others 2001). Primary production was higher 10-yrs after a debris flow, but biomass was lower (Cover and others 2010). However, responses return to pre-disturbance levels as forests regenerate (Minshall and others 2001; Cover and others 2010), and we expect that autotrophs would respond similarly to beetle outbreaks due to comparable trends in tree mortality and regeneration. Given the importance of tree regeneration for post-disturbance recovery of stream primary production, reduced forest regeneration may sustain higher light flux and production over longer periods (Table 2). However, changes also may reduce primary production. As wildfire and debris flows can increase sediment inputs (Pierce and others 2004), they may increase turbidity, which can attenuate light flux to the benthos and reduce primary production (Young and Huryn 1996; Izagirre and others 2008). Sediment also can increase abrasion and reduce algal biomass (Biggs and others 1999; Francoeur and Biggs 2006). 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), suggesting increased sediment inputs could decrease production by reducing light flux to the benthos and increasing abrasion (Table 2; Fig. 3).

The net response of autotrophic production will depend on the relative magnitude of the positive (e.g., light) and negative (e.g., 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, we speculate that the net effect of these factors will ultimately increase primary production more than would be expected based on direct effects alone (Table 2; Fig. 3).

*Heterotrophic microbial production*: As temperature and flow contribute to regulating microbial production and respiration (Uehlinger 2000; Allen and others 2005), CC is expected to directly alter production of heterotrophic microbes (i.e., fungi and bacteria; hereafter referred to as ‘microbes’). In short-term experiments, higher water temperatures increased microbial production and respiration, but respiration increased more (Sand-Jensen and others 2007). However, microbes can exhibit thermal adaptation such that respiration may be resilient to temperature increases, as has been shown by long-term soil warming experiments (Bradford and others 2008). Increases in respiration also may be transitory if it is ultimately limited by photosynthesis and the processes are in steady state (Allen and others 2005). Yet, respiration in many streams is not limited by aquatic primary production because microbes rely on inputs of terrestrial or stored organic matter (Mulholland and others 2001). In such cases, respiration increases may be sustained (Yvon-Durocher and others 2010). Because warming is expected to increase microbial respiration in heterotrophic streams (Acuna and Tockner 2010; Boyero and others 2011) and many forested streams are heterotrophic, microbial production may increase in forested streams considered in our model. Such thermal effects may be attenuated by more frequent floods because floods, in general, decrease microbial respiration and production (Uehlinger and Naegeli 1998; Uehlinger 2000). Hence, CC will directly affect microbial responses via altered temperature and flow (Table 2; Fig. 3).

Terrestrial processes will likely alter microbial responses as they can affect factors important for maintaining microbial populations (e.g., nutrients, substrate stability, detritus availability; Bott and others 1985; Uehlinger 2000; Findlay 2010). Reduced inputs of terrestrial organic matter may increase resource limitation of microbes, but increases in aquatic primary production could stimulate microbial production. However, an interbiome comparison of streams found a weak relationship between respiration and primary production (Mulholland and others 2001), indicating that increased primary production may have little impact. Also, microbial activity in a forested stream of eastern North America, as measured by ecosystem respiration (ER), was primarily regulated by leaf detritus availability and was weakly related to temperature (Roberts and others 2007). Consequently, assessments of microbial responses should integrate changes in inputs and retention of organic matter, which can be affected by large wood and interactions between fire and flow (Gurnell and others 2002; Arkle and others 2009). Wildfire can increase organic matter retention and microbial respiration up to 20 yrs post-fire (Robinson and others 2005); however, we expect that microbial production will decrease over longer time scales. For instance, high flows decreased organic matter and wood standing crop in burned, but not in unburned streams (Arkle and others 2009), patterns that also may be observed after large-scale beetle outbreaks. Reduced forest regeneration will also likely decrease microbial production. As detritus inputs and standing crop were lower in shrub-grassland streams (Webster and Meyer 1997), reduced forest regeneration and altered disturbance regimes may decrease detritus availability, especially if wood inputs decrease. Altered terrestrial processes may amplify resource limitation of microbes, subsequently decreasing their production despite increases expected in response to temperature and precipitation alone (Table 2; Fig. 3).

*Consumer production:* Temperature increases are predicted to reduce taxa richness (Durance and Ormerod 2007) and alter community composition of stream animals (Poff and others 2010), but biomass and production responses are uncertain (Hogg and Williams 1996; Durance and Ormerod 2007). Biomass may decline because warming can increase respiration rates, reducing growth efficiency and body size (Sweeney 1978; Woodward and others 2010). Secondary production, which integrates several consumer metrics (i.e., abundance, biomass, and growth rate), may subsequently increase due to higher temperatures and smaller body sizes (Fig. 3; Benke and Huryn 2010). Thus, stream warming may decrease consumer biomass, but increase production (Table 2).

Shifts to a rain-dominated hydrology will likely affect consumers (Poff and others 2010). As many stream biota in western North America adapted to past flow regimes that exhibited low winter flow and predictable spring run-off, they developed life-history traits to minimize impacts of seasonal high flows (Harper and Peckarsky 2006). However, earlier spring run-off can decouple ecological cues, reduce populations of taxa that depend on predictable flow (Harper and Peckarsky 2006; Poff and Zimmerman 2010), and increase populations of those resistant to substratemobilizing floods (Poff and others 2010). Because many disturbance-resistant taxa are small-bodied (e.g., Chironomidae larvae; Benke and Huryn 2010), shifts in flow regime that reduce substrate stability may increase production. For example, although biomass was similar, secondary production was ca. 1.6× greater in an Idaho stream with ca. 12× greater flow variability than in a paired stream; differences were driven by dominance of disturbance-resistant taxa (Robinson and Minshall 1998). Sycamore Creek, an open-canopy desert stream in the southwestern United States, also had high production despite high thermal and flow variability (Jackson and Fisher 1986). Thus, shifts in flow regime may alter composition, reduce biomass, and increase secondary production (Table 2; Fig. 3).

Terrestrial processes will likely affect consumer production in streams as it is governed by many factors (i.e., food quantity and quality, temperature, flow, and substrate stability; Benke and Huryn 2010; Poff and Zimmerman 2010) that are predicted to change. Wildfire may increase consumer production because it can increase the biomass (Minshall and others 2001; Malison and Baxter 2010) and dominance of disturbance-resistant taxa (Vieira and others 2004; Romme and others 2011). In addition, some coldwater-adapted taxa can persist in burned streams, despite warmer stream temperatures (Dunham and others 2007). Consumer biomass and production were also higher in open vs. closed canopy streams, likely due to greater autotroph production (Behmer and Hawkins 1986; Kiffney and others 2004); effects that may be mirrored when beetle outbreaks decrease tree cover. Thus, increases in consumer respiratory demands and thermal stress expected with CC (Woodward and others 2010) may be partly offset by greater autotrophic production, increasing their production more than would be predicted from direct effects alone (Fig. 3).

Although terrestrial processes may increase consumer production via some mechanisms, these changes also may have negative consequences for consumers. Sedimentation can be an important source of stream impairment that negatively affects many stream consumers (Waters 1995). Fine sediment fills in interstitial habitat in the substrate and decreases oxygen availability, subsequently increasing mortality (Waters 1995; Bilotta and Brazier 2008). One study reported sediment-resistant taxa dominated burned watersheds, whereas unburned streams were dominated by sediment-sensitive taxa (Arkle and others 2009). Sensitive taxa have been found in some streams scoured by debris flows (Dunham and others 2007), but other evidence indicates that these channels can be devoid of sensitive taxa (Cover and others 2010). Such evidence indicates that terrestrial processes may contribute to extirpation of sensitive taxa and increase dominance of sediment-resistant taxa.

As terrestrial detritus can support detritivore production (Wallace and others 1999), expected declines in detritivore populations due to warming (Boyero and others 2011) may be magnified by lower inputs of organic matter. Wildfire reduced populations of taxa that specialize on terrestrial detritus, increased populations of diet generalists (Mihuc and Minshall 1995; Minshall and others 2001), and increased reliance on autotrophic resources (Spencer and others 2003). Also, debris flows largely extirpated detritivores, likely due to lower detritus availability (Cover and others 2010). Reduced detrital inputs and retention may decrease production of obligate detritivores and increase production of algivores or diet generalists that can exploit autotrophic resources (Table 2; Fig. 3).

Alteration of terrestrial processes may stimulate consumer production, increase the dominance of disturbance-resistant taxa, and shift community composition toward algivores and diet generalists (Table 3). Such a possibility is supported by greater secondary production and dominance of disturbance-resistant taxa in desert streams, which often experience frequent floods, increased light flux, and higher primary production (Jackson and Fisher 1986; Mulholland and others 2001). Given considerable evidence that CC is increasing the frequency of these disturbances known to affect consumer populations (Westerling and others 2006; Cover and others 2010; Romme and others 2011), these disturbances should be considered when assessing consumer responses to CC.

*Ecosystem metabolism*: Based on direct effects of temperature and flow, streams may become more heterotrophic and exhibit lower net ecosystem production (NEP), the difference between ER and gross primary production (GPP) (Acuna and Tockner 2010; Yvon-Durocher and others 2010). Warming can stimulate GPP and ER, but ER can exhibit larger increases (Yvon-Durocher and others 2010). Conversely, more frequent winter floods may decrease GPP and ER because, in general, they are negatively related to flood frequency (Uehlinger and Naegeli 1998). Yet, ER declines may be smaller as it mostly occurs in the hyporheic zone, where it is less susceptible to scour (Uehlinger and Naegeli 1998; Uehlinger 2000). Therefore, effects of more frequent floods and warming may reinforce each other in the winter, decreasing GPP more than ER and increasing heterotrophy (Table 3; Fig. 3). In contrast, GPP and autotrophy may increase as CC will likely reduce summer baseflow (Young and others 2008; Marcarelli and others 2010). Despite contrasting seasonal responses, CC has been predicted to decrease NEP (Yvon-Durocher and others 2010).

Shifts in terrestrial processes may alter metabolic responses because light and organic matter are drivers of stream metabolism (Bott and others 1985; Mulholland and others 2001). A cross-biome comparison showed that light, nutrients, and temperature explained 90% of variation in GPP and light alone explained 53% of the variation in NEP (Mulholland and others 2001). For instance, GPP was substantially lower in a coniferous forested stream (77 - 148.3 g $m^{-2}$ $yr^{-1}$) than in Deep Creek (3,540 g $m^{-2}$ $yr^{-1}$), an open-canopy shrub-grassland stream in Idaho (Minshall 1978; Webster and Meyer 1997). In a forested stream of eastern North America that exhibits strong heterotrophy, GPP increased after a spring freeze that delayed canopy closure and increased light flux (Mulholland and others 2009). As light can promote post-scour recovery of GPP (Uehlinger 2000), reductions in canopy cover due to CC may ameliorate expected declines in GPP due to frequent floods. In fact, Sycamore Creek, which experiences frequent floods, was the only stream across many regions that was autotrophic and had positive NEP, likely due to higher light flux (Mulholland and others 2001). Conversely, increased sediment inputs and reduced organic matter inputs may attenuate light effects. Sedimentation reduced light flux to the benthos, decreasing GPP and increasing heterotrophy during years with high flow and turbidity (Young and Huryn 1996). Reduced terrestrial organic matter inputs also may reduce ER because organic matter standing crop can be a primary regulator of ER (Roberts and others 2007). Differences in organic matter standing crop may be why ER was related to temperature in one cross-biome comparison (Mulholland and others 2001), but not in another (Bott and others 1985). Thus, CC-induced shifts in terrestrial processes may attenuate ER increases, GPP reductions, and greater heterotrophy expected based on thermal and flow effects alone (Table 3; Fig. 3). However, there are substantial uncertainties in predicting responses of metabolism to GCC, indicating the need for further studies that address both direct and indirect mechanisms.

*Carbon export:* Temperature and flow shifts may have contrasting effects on carbon export. Downstream export may decline because higher temperatures can increase microbial respiration and the proportion released as $CO_2$ (Acuna and Tockner 2010; Yvon-Durocher and others 2010; Boyero and others 2011). On the other hand, warming may increase export because greater microbial production can be fueled by processing carbon stored in sediments (Acuna and Tockner 2010; Gudasz and others 2010). A space-for-time comparison also found that carbon uptake was related to periphyton biomass and stream width/depth ratio, but not temperature, light, or GPP (Marti and others 2009). Therefore, faster processing due to warming may not be offset by uptake, reducing retention efficiency. Because export is positively related to discharge (Wallace and others 1991) and flow variability and high flows can alter carbon dynamics more than temperature (Acuna and Tockner 2010), export may increase in the winter, but decrease in the summer. Greater flow variability expected with rain-dominated hydrology may override warming effects (Table 3; Fig. 3).

Terrestrial processes may mediate responses of export expected based on temperature and flow alone. Terrestrial detritus can be an important source of carbon pools and export (Webster and Meyer 1997), so export may decline due to lower carbon inputs. Conversely, fewer wood inputs may increase export because wood is important for organic matter retention in high-gradient streams of western North America (Megahan 1982; Gurnell and others 2002). Storage of sediment and associated organic matter is positively related to instream wood volume (May and Gresswell 2003) and wood stored 15-yrs of sediment and organic matter in Idaho streams (Megahan 1982). This suggests that altered terrestrial processes may decrease export due to lower carbon inputs; buy may increase it via declines in woody debris. Although the net response of export is unclear and requires further study to fully assess, our analysis points to pathways by which terrestrial processes could attenuate or magnify responses based on direct effects alone (Table 3; Fig. 3).

## Conclusion

Results from our ecosystem model suggest that in ecoregions where CC is shifting ecosystem distributions and increasing natural disturbance activity the effects of CC will not be limited to the direct effects of changing temperature and flow. As changes in terrestrial processes are likely altering the ecological context in which CC is occurring, such indirect effects need to be integrated into our understanding of CC. However, our analysis identified uncertainties in some responses (e.g., export and metabolism); thus, it highlights the need for further studies that explicitly assess their responses to the direct and indirect effects of CC. Similar to the way that the incorporation of disturbance regimes and vegetation changes can inform predictions about temperature increases and the global carbon cycle (Goetz and others 2007; Kurz and others 2008), their incorporation may improve understanding of how stream organisms and ecosystem processes will respond to CC. Despite some difficulties in incorporating terrestrial processes into CC predictions, their exclusion poses greater problems because CC is altering these processes known to influence streams.

Although our analysis focused on north temperate forested streams, CC is altering ecosystem distributions and disturbance regimes in a variety of regions, indicating the broad applicability of our approach. Similar analyses applied to other regions would further elucidate unanticipated effects of CC on streams. For instance, wildfire activity is increasing globally (Flannigan and others 2009), as evidenced by predictions that wildfire area may increase 3-5× (Dury and others 2011) and fire return intervals may shorten in the Mediterranean, changes that may eliminate woody species and convert these ecosystems to grass-dominated ecosystems (Malkisnon and others 2011). Also, CC is expected to increase the extent of insect outbreaks in a range of ecoregions, such as hemlock wooly adelgid beetles (*Adelges tsugae*) in eastern North America and spruce bark beetles (*Ips typographus*) in Europe (Jonsson and others 2007; Dukes and others 2009). Ecosystem boundaries also are projected to move on a worldwide basis due to changes in climate and disturbance regimes (Frelich and Reich 2010; Gonzalez and others 2010), with evidence that shifts can sometimes occur rapidly (Turner 2010; Clifford and others 2011). As even small shifts in the composition of vegetation communities may affect streams (Ball and others 2010), the effects of CC may be substantially underestimated when terrestrial processes are not considered, even when CC does not lead to wholesale changes in ecosystem distributions. Such widespread evidence indicates the importance of integrating both potential direct and indirect effects of CC into predictive frameworks that assess stream responses.

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**Table Legends:**

**Table 1:** Predicted stream responses to changes in temperature / precipitation regimes and terrestrial processes (i.e., wildfire, insect outbreaks, debris flows, and altered vegetation structure). Positive, negative, and neutral responses indicated by (+), (-), and (0), respectively.

**Table 2:** Predicted stream responses to changes in temperature / precipitation regimes and terrestrial processes (i.e., wildfire, insect outbreaks, debris flows, and altered vegetation structure). Symbol designations as in Table 1.

**Table 3:** Predicted stream responses to changes in temperature / precipitation regimes and terrestrial processes (i.e., wildfire, insect outbreaks, debris flows, and altered vegetation structure). Symbol designations as in Table 1.

Table 1

| **Stream parameter** | **Effects of temperature/precipitation** | **Effects of terrestrial processes** | **Net Response** |
|---|---|---|---|
| Stream temperature | **(+)** Increased atmospheric temperature will increase stream temperatures | **(+)** Terrestrial processes that reduce canopy cover will increase stream temperatures | **(+)** Terrestrial processes will reinforce temperature responses, warming streams more than direct effects alone |
| Light flux | **(0)** | **(+)** Terrestrial processes that reduce canopy cover will increase light availability | **(+)** Terrestrial processes will be more important, increasing light flux more than direct effects alone |
| Nutrient input | **(+)** Reduced winter snowpack that increases soil freezing will increase soil nutrient leaching and inputs to streams | **(0)** Terrestrial processes can increase short-term inputs, but have no effect over long-term | **(+)** Temperature/precipitation effects will be more important, increasing nutrient inputs |
| Sediment input | **(0)** | **(+)** Greater disturbance activity will increase long-term sediment inputs, especially when forests don't regeneratre | **(+)** Terrestrial processes will be more important than direct effects, increasing sediment inputs more than direct effects alone |
| Organic matter (OM) input | **(0)** | **(+)** If forests regenerate, greater disturbance activity will increase OM inputs<br>**(-)** If forests do not regenerate, greater disturbance activity will reduce inputs of terrestrial OM | **(-)** Terrestrial processes will be more important, decreasing OM inputs more than direct effects alone |
| Large-woody debris (LWD) input | **(0)** | **(+)** If forests regenerate, greater disturbance activity will increase LWD inputs<br>**(-)** If forests do not regenerate, greater disturbance activity will reduce LWD inputs | **(-)** Terrestrial processes will be more important, decreasing LWD inputs more than direct effects alone |

Table 2

| **Stream parameter** | **Effects of temperature/precipitation** | **Effects of terrestrial processes** | **Net Response** |
|---|---|---|---|
| Autotrophic production | **(+)** Higher temperatures will stimulate algal production<br>**(-)** More frequent scour will decrease algal productivity | **(+)** Increased light flux associated with reduced canopy cover will increase productivity.<br>**(-)** Increased sediment inputs will increase scour and turbidity, reducing productivity | **(+)** Despite increased scour and turbidity, terrestrial processes that increase temperatures and light flux may offset expected declines associated with scour, increasing autotrophic productivity |
| Heterotrophic microbial production | **(+)** Higher temperatures will stimulate microbial production<br>**(-)** More frequent scour will decrease productivity, but declines may be minimized because the hyporheic zone is relatively scour resistant | **(-)** Reductions in OM and LWD inputs will reduce detritus standing crop and increase resource limitation, reducing microbial production | **(-)** Terrestrial processes that increase detrital resource limitation may offset, or exceed, effects of higher temperatures, decreasing microbial production |
| 1° and 2° consumer production | **(+)** Higher temperatures will increase consumer production.<br>**(+)** More frequent scour will increase the dominance of small-bodied disturbance-resistant taxa, increasing consumer production | **(+)** Increased algal productivity will increase herbivore production<br>**(-)** Reduced OM and LWD inputs and retention will decrease detritivore production<br>**(+)** Increased sedimentation that increases disturbance-resistant taxa will increase production | **(+)** Terrestrial processes will reinforce temperature and scour effects. They will increase consumer production and shift consumer community composition toward taxa that are disturbance-resistant and can utilize autotrophic production |

Table 3

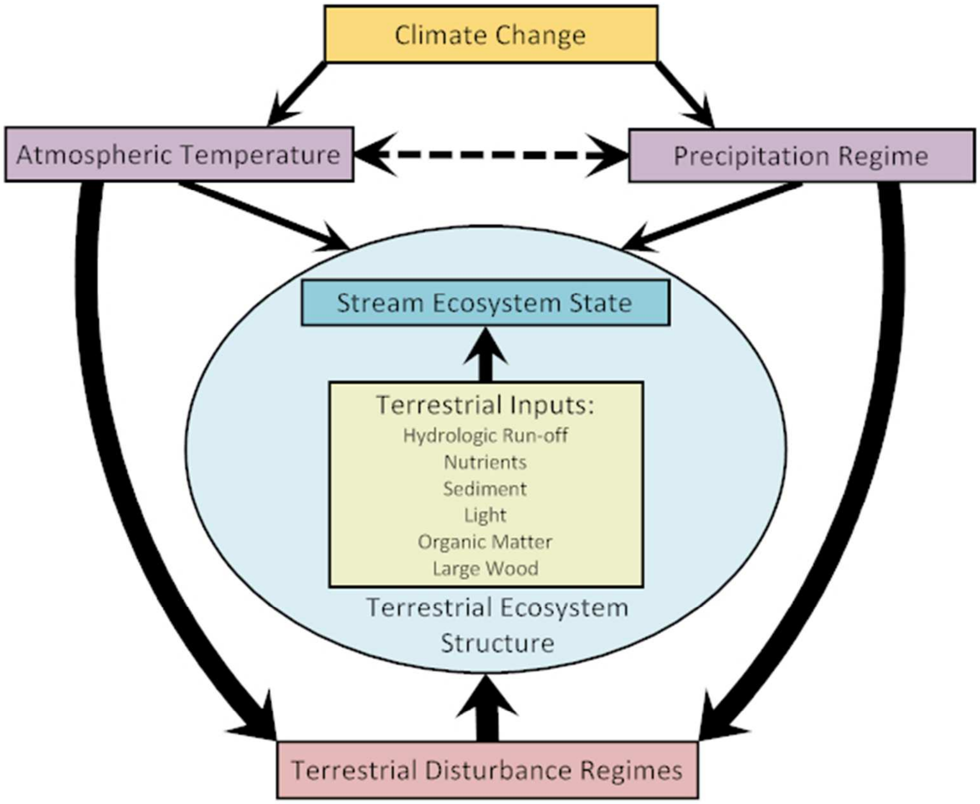
| **Stream parameter** | **Effects of temperature/precipitation** | **Effects of terrestrial processes** | **Net Response** |
|---|---|---|---|
| Net ecosystem production (NEP) | **(-)** Higher temperatures will increase ecosystem respiration (ER) more than gross primary production (GPP), decreasing NEP<br>**(-)** More frequent winter scour will reduce GPP more than ER, decreasing winter NEP<br>**(+)** Lower summer baseflow may increase GPP more than ER, increasing summer NEP | **(+)** Increased light flux will increase GPP more than ER, increasing NEP<br>**(-)** Increased sediment inputs will increase turbidity, attenuating light-induced increases in GPP and decreasing NEP | **(+)** Increased light flux and lower base flows may offset expected NEP declines due to temperature increases, increasing NEP<br>**(-)** If increased turbidity attenuates light to the substrate, terrestrial processes may reinforce temperature and scour responses, decreasing NEP |
| Carbon export | **(+)** Higher temperatures can increase microbial processing of stored benthic carbon, increasing downstream export<br>**(+)** Shifts to a rain-dominated hydrology that increase winter baseflow will increase winter carbon export<br>**(-)** Shifts to a rain-dominated hydrology that decrease summer baseflow may decrease summer export | **(-)** Reductions in terrestrial OM inputs will reduce sources of stream carbon, reducing export<br>**(+)** Reductions in terrestrial LWD inputs will reduce structures important for carbon retention, increasing carbon export | **(+)** Fewer retention structures may magnify effects of winter scour and temperature, increasing carbon export<br>**(-)** Reductions in terrestrial OM may reinforce declines due to lower summer baseflow, decreasing export |

## Figure Legends

**Fig. 1:** Conceptual model of the direct and indirect effects of climate change (CC) on stream structure and function. CC will alter temperature and precipitation regimes, with consequences for stream ecosystems. However, expected shifts in temperature and precipitation regimes will increase the frequency and spatial extent of terrestrial disturbances (e.g., drought, wildfire, debris flows, and insect outbreaks) that will change terrestrial ecosystem regeneration and structure. These shifts in terrestrial processes will alter terrestrially-derived resource inputs (i.e., run-off, nutrients, sediment, light, and organic matter). Arrow widths are proportional to expected effects. Dotted arrow represents the coupling of atmospheric temperature and precipitation regime responses.

**Fig. 2:** Projected response and recovery of (A) light flux, (B) sediment inputs, and (C) large wood inputs under past climate conditions that facilitated forest regeneration post-disturbance (typically within ca. 100-200 years; dotted line) versus when forest is converted to shrub-steppe ecosystem (solid line). Solid arrows represent the initial wildfire, while dotted arrows represent subsequent wildfires if forests are converted to shrub-steppe ecosystems (ca. 70 yr fire return interval).

**Fig. 3:** Ecosystem model indicating pathways by which CC-induced shifts in temperature, precipitation, and terrestrial processes (e.g., disturbance regimes and ecosystem distributions) may alter streams. For each pairwise comparison that described the effect of a factor on a response variable, we assessed whether the effect was positive (green arrow), negative (red arrow), or neutral (black arrow) during the period of response (150-200 years). Dotted arrows were used when an effect existed, but its direction was unknown. By summing the various factors (i.e., arrows) affecting a given response, we predicted if it would increase (green box) or decrease (red box) when all direct and indirect pathways were considered. We could not predict directions of change for all arrows affecting a response. However, when the unknown arrows were unlikely to offset known effects, predictions were made based on stream ecology principles and shading indicated lower confidence.



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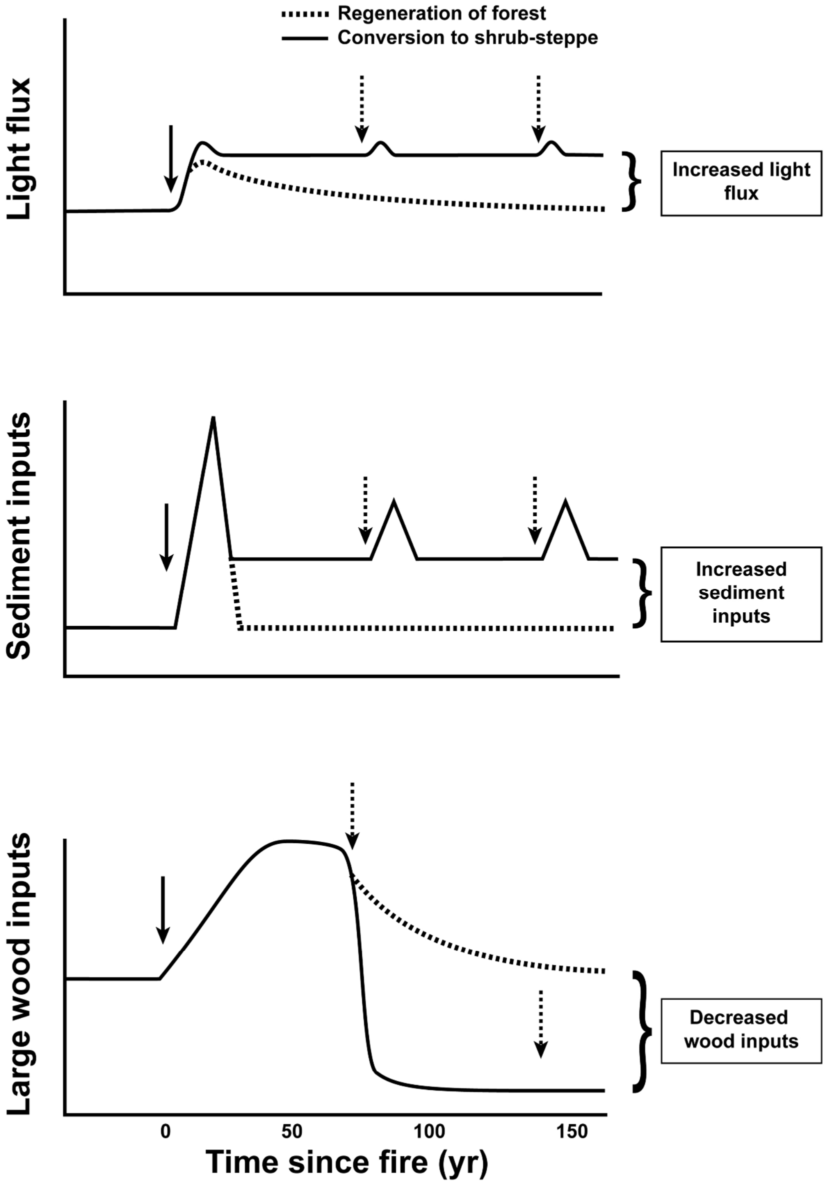

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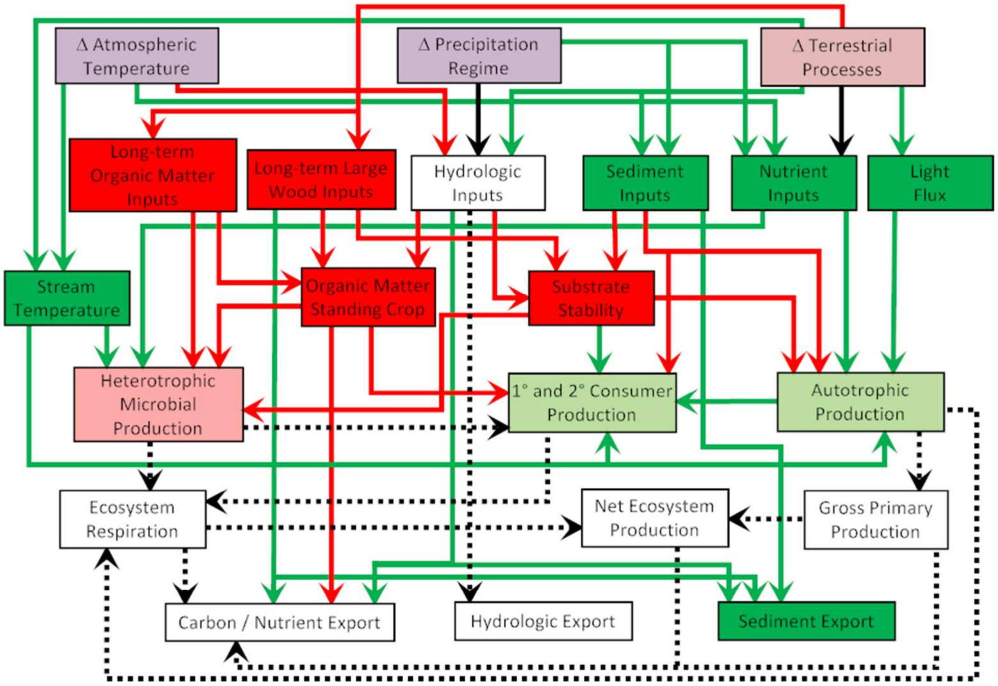

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