



# Ecohydrology and Climate Change in the Mountains of the Western USA – A Review of Research and Opportunities

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## Abstract

Snow-dominated mountain regions are strategic providers of water resources and ecosystem services. They are also likely to be highly vulnerable to a warming climate. In this review, we argue that an ecohydrologic perspective is critical for understanding changes that are already occurring and ultimately for predicting future vulnerabilities in both water resources and ecosystem health. We focus our review on the relatively well-studied mountains of the Western USA. In this region, observations and models show significant climate-driven changes to hydrologic processes including changes to snow accumulation and melt, evapotranspiration, soil moisture, and streamflow. At the same time, there is growing evidence of climate-driven changes in vegetation structure and function. We summarize these studies and discuss how changes in hydrology interact with changes in terrestrial ecosystems to lead to complex and sometime synergistic responses. We conclude by identifying research needs to be addressed by emerging monitoring and synthesis networks that focus on the ecohydrology of mountain environments within a changing climate.

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## Introduction

The largest changes in the hydrologic cycle with climate warming are expected to occur in mid- to high-latitude snow-dominated regions (Barnett et al. 2005). A growing literature on the hydrologic response to warming in the Western USA and other mountain regions highlights changes in the timing of runoff associated with reduced snow accumulation and earlier melt (Bales et al. 2006). Model predictions and empirical analysis of long-term trends also predict changes in total runoff, soil moisture, and evapotranspiration (ET) with warming, but these changes show less consistency in both magnitude and direction of response. Changes in total runoff, soil moisture, and ET with warming are directly tied to ecological responses, as plant-related ET accounts for a significant proportion of the water budget except in very high-elevation watersheds (i.e. above the treeline). Understanding how vegetation water use will change with warming in snow-dominated mountain environments requires taking a coupled eco-hydrologic perspective. For hydrologists, there is a need to understand and ultimately quantify how potential changes in vegetation structure and function may dampen or amplify changes in the timing and magnitude of streamflow associated with warmer temperatures. For ecologists, there is a need to understand how vegetation communities will respond to changes in the hydrologic cycle, including reduced and earlier snowmelt, changes in precipitation, as well as interactions among radiation, temperature, and vapor pressure deficits as drivers of ET.

In this review article, we summarize recent literature on the controlling processes of coupled eco-hydrologic responses to climate warming, particularly in mid-latitude snow-dominated mountain environments. We focus our review on the well-studied Western US mountain region (Figure 1), but many of these findings will be applicable to other snow-dominated temperate mountain regions with similar maritime climate and steep terrain throughout the globe. In assessing ecohydrologic responses to warming, there are several factors that are distinct to mountain environments. First, mid-latitude mountain regions are typically snow-dominated for some portion of the landscape and season. Changes in snow accumulation and melt with warming are therefore key components of ecohydrologic response. Mountain regions are usually characterized by strong topographic gradients, which are likely to cause significant spatial variation in responses to warming. Different locations will have different magnitudes and in some cases different directions of ecohydrologic response to a warming climate. These spatial differences may either moderate or exacerbate the effects of warming on cumulative watershed fluxes such as streamflow. Mountain drainage characteristics, in particular steep topographic gradients leading to relatively rapid drainage, also play a role in determining how the system will respond. For example, ecohydrologic impacts of climate change in relatively flat, sub-arctic boreal regions will be strongly influenced by permafrost melting and associated redistribution of moisture (Woo et al. 2008). Increased inundation is less important in mountain environments with their steep drainages. Mountain environments are thus unique systems in their ecohydrologic responses to climate warming. Further, these environments are not only highly sensitive to climate change, but mountain ecotones may provide some of the earliest opportunities to detect and study climate change impacts.



Fig. 1. Map of the Western US Mountain Region.

### *Changing Snow Accumulation and Melt with Warming*

One of the most commonly cited impacts of a warming climate in mountain environments is a reduction in snow accumulation and earlier melt. Throughout the mountains of the Western USA, empirical analyses have identified statistically significant trends toward earlier timing of snowmelt (Stewart et al. 2005) and increasing proportion of precipitation falling as rain versus snow (Knowles et al. 2006). Model-based analyses project continued shifts in the timing of melt to earlier in the year along with a rising rain-to-snow transition zone (Knowles and Cayan 2004; Nolin and Daly 2006). The geography of changing snowpack with warming in the Mountain West is dominated by elevational and latitudinal controls on climate. Areas where a significant proportion of seasonal snow currently falls during temperatures near the freezing point are the most vulnerable (Mote et al. 2005; Nolin and Daly 2006). For example, Leung et al. (2004) show that much of the coastal ranges, which have moderate elevations and more maritime climate, would lose the majority (~60% to 70%) of their seasonal snowpack under even moderate warming. In contrast, the higher elevation Rocky Mountains, with more continental climate, show relatively moderate (~20%) changes in snow accumulation and melt with moderate warming. Adam et al. (2009) argue that these same trends observed and predicted in the Western USA are relevant to a wider domain. Using a global hydrologic model forced with ensemble general circulation model (GCM) predictions for climate under a 'business as usual' emissions scenario, they found that temperature increases lead to widespread and substantial decreases in winter snowpack and spring snowmelt independent of precipitation changes (Adam et al. 2009).

### *How Changes in Snow Translate into Changes in Streamflow*

Reduced snow accumulation and earlier melt lead to changes in the seasonality of streamflow (see Figure 2 for an illustration of these effects). In the Western USA, where the

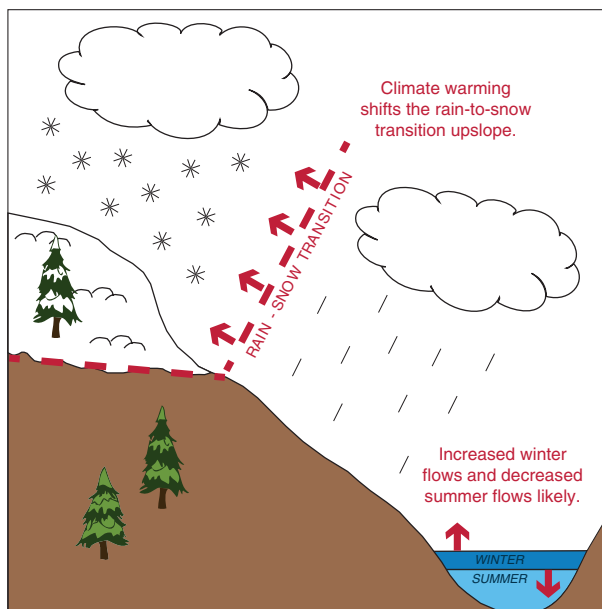


Fig. 2. Illustration of potential climate change impacts on snow with implications for streamflow in temperate mountain watersheds.

majority of precipitation falls during the winter months, snowpack temporarily stores water; earlier melt or more winter precipitation occurring as rain means that this water leaves as streamflow earlier in the year. Stewart et al. (2005) show that the center of mass of streamflow is, since the 1950s, occurring earlier for 86 of 96 streams in a set distributed throughout in the Western USA. The magnitude of these timing shifts was highly variable, ranging from several days up to 4 weeks. Rood et al. (2008) also show earlier peak flows and lower summer flows for a wide range of streams in the Rocky Mountains. Trends toward increased winter flow, earlier spring flow, and reductions in summer flow are also predicted by coupled GCM-hydrologic models (Maurer 2007). All these analyses show high spatial heterogeneity in the magnitude of responses and, for the empirical analyses, the statistical significance of trends. For example, Rood et al. (2008) show shifts in summer streamflow ranging from no change to reductions of 30% in the past few decades. Spatial differences in the vulnerability of snow explain some of this variation, but other factors, most notably geology, have been shown to exert important controls on how changing snowpack translates into changes in seasonal hydrographs. Tague and Grant (2009) show that spatial differences in geologically mediated drainage rates are a first-order control on the sensitivity of summer streamflow to warming and suggest that slower draining systems, such as the High Cascades of Western Oregon, will show greater volume reductions in August streamflow for a given reduction in snowpack. It is likely that adaptation in the seasonality of vegetation water use may also contribute to how changing snow accumulation and melt alter seasonal hydrographs, but this has not been explicitly studied.

### *Changes in Precipitation Patterns and Streamflow*

Although changes in snow accumulation and melt are important drivers of changes in streamflow, interannual and seasonal variabilities in streamflow are dominated by patterns of precipitation. Global change is likely to alter precipitation patterns; however, GCM predictions of future precipitation shifts are uncertain and highly variable for the Western USA and elsewhere. Regionally coherent changes in observed trends in precipitation are challenging to demonstrate given limited data availability and high spatial heterogeneity. Streamflow, in particular annual streamflow, is highly correlated with annual precipitation and, by spatially integrating precipitation over a catchment area, can often reveal regional patterns better than individual measurement points alone. Taking advantage of this relationship, streamflow in unregulated, unaltered basins has been used as a proxy to demonstrate historical changes in precipitation.

In the Western USA, an analysis of streamflow records in Idaho, western Wyoming, and northern Nevada shows the majority of stations experiencing declines in annual mean streamflow (Clark 2010). Other broader regional studies, however, do not show widespread significant trends in mean annual streamflow (Luce and Holden 2009; Pagano and Garen 2005). Pagano and Garen (2005) do show that recent decades have higher variability and higher persistence in annual flows relative to earlier periods. Thus, although trends in mean annual streamflow are equivocal, in part due to high interannual variation in precipitation, the frequency of multiyear droughts appears to be increasing. Building from these observed trends in temporal patterns of annual streamflow, Luce and Holden (2009) attribute the observed recent increase in interannual variability to a declining trend in the magnitude of low flows (specifically 25th percentile flows), indicating that dry years are becoming drier. The authors suggest that these changes, although associated with regional Pacific Decadal Oscillation and El Niño Southern Oscillation cycles, may also reflected a longer-term climate trend. Combined, these observed trends in decreasing low flows and

higher year-to-year persistence can have important ecological consequences, such as documented evidence of forest mortality often associated with multiyear droughts (Allen et al. 2010). It is important to note that changes in the amount of precipitation can also impact the seasonal timing of water availability. Low snow years will have earlier melt even without climate warming and consequently shift the center of mass of streamflow to earlier in the year (Moore et al. 2007; Tague and Grant 2009). Luce and Holden (2009) demonstrate that total discharge is a better predictor of timing of flow than long-term trends in timing that have been attributed to warming. This additional control on timing means the impact of low precipitation years, and in particular multiyear low precipitation years (high persistence), will be particularly evident during the summer when ecosystems are vulnerable to low water availability as both soil moisture and streamflow.

#### *Climate-driven Changes in ET at the Continental Scale*

On an annual basis, however, linkages between climate change driven shifts in the timing of vegetation water use and changes in annual streamflow have been established as important responses (Barnett et al. 2005). Changes in total ET and consequently annual runoff under climate change scenarios are expected to be functions of changes in precipitation, humidity (drier air with warmer temperatures), irradiance (cloudiness), and wind speed (Barnett et al. 2005). At the same time, coupled land-surface GCM models (Betts et al. 2007) demonstrate that increasing CO<sub>2</sub> concentrations may increase plant water use efficiency, increase stomatal closure, and reduce ET over broad continental scales. Whether changes in ET, in particular climate-based changes in vegetation water use, have altered broad-scale streamflow patterns continues to be an area of research and debate (Dai et al. 2009; Labat et al. 2004; Legates et al. 2005). Recent empirical analysis of monthly streamflow records across the globe suggests continental scale inter-annual variation and trends in runoff are largely dominated by precipitation (rather than CO<sub>2</sub> or land use/land cover changes). Dai et al.'s (2009) analysis does show that there is evidence of decreasing discharge from rivers draining into the Pacific that may reflect an increase in ET with aridity in addition to precipitation changes. Only the Arctic Ocean shows trends of increasing discharge that can be explained largely by changes in ice and snowmelt. Although these results suggest precipitation remains the dominant driver at coarse spatial scales and relatively short time scales, long-term streamflow responses of individual watersheds within mountain environments may be more sensitive to vegetation change. At continental scales, there is likely to be a diversity of vegetation water use responses to warming with both increases and decreases that may counterbalance to reduce aggregate impacts. Further, at continental scales, vegetation responses to warming may be obscured by other land use dynamics. At more local scales, vegetation response may in some cases be more spatially coherent. In mountain environments, energy and water limitations interact in complex ways and changes in snow dynamics play a dominant role, potentially amplifying changes in vegetation structure and function and ultimately streamflow. Establishing linkages between streamflow and vegetation change may be more tractable at the sub-regional scale, and this level of detail may in fact be necessary as a high degree of response variability suggests that we need to explicitly consider the local geo-climatic and ecosystem settings.

#### *Vegetation Productivity, Water Use, and Climate Change*

The consequences of warming for vegetation water use depend on a complex interplay between atmospheric drivers, plant physiological responses to temperature, moisture



availability, increased CO<sub>2</sub>, and linkages with disturbances including fire and disease. For mountain environments all these controls are important, but their relative importance and interactions are likely to vary across relatively short spatial scales. Vegetation response also occurs across a range of time scales, with short-term responses (such as increased ET with higher vapor pressure deficit) interacting with intermediate time scale responses (changes in growth rates) and longer-term responses (changes in stand structure and composition). All these changes in vegetation structure and function have the potential to alter vegetation water use and consequently soil moisture and streamflow. An important concept in thinking about ecohydrologic responses to warming is the 'optimality hypothesis', which states that stand structure will adapt to make best use of available resources (Eagleson 1982). If the optimality hypothesis holds then, in primarily water-limited environments, increases in water use efficiency with elevated CO<sub>2</sub> will not translate into increases in streamflow because biomass will increase to use additional water (Kozłowski 2000). Optimality, however, does not preclude changes in vegetation water use if other factors, such as temperature, are limiting or if disturbance plays a key role in vegetation biomass or composition and associated water use, both of which may be the case in mountain environments. To summarize recent research on these ecohydrologic interactions, we begin by considering evidence that vegetation structure (biomass) and composition are changing and may continue to change in Western US mountain environments. We then highlight how many of these changes in vegetation are tightly coupled with hydrologic changes and may alter downstream flows.

Boisvenue and Running (2006) provide a global review of changes in forest biomass over the past five decades and linkages with climate. Their review combines field and remote sensing based measurements of forest biomass. Generally, both sources show increases in forest productivity since the middle of the 20th century except in water-limited environments. Regional studies within the Western US mountains parallel these global trends. Tree ring analyses of forests in the Cascade and Sierra ranges suggest a transition between higher elevations that show increased growth in warmer years and lower elevations that show decreased growth in drier years (Bunn et al. 2005; Case and Peterson 2005; Nakawatase and Peterson 2006). Analyses of recent trends over the past one to two decades typically show increases in growth and forest biomass at high elevations (Klasner & Fagre 2002; Millar et al. 2004), although forests have not shifted to locations above the treeline (Fagre et al. 2003).

An outstanding question is whether the observed increases in growth are due to climate factors or shifts in other resource availability, such as increased CO<sub>2</sub> fertilization (see Figure 3 for an illustration of potential effects). Sites most sensitive to elevated CO<sub>2</sub> are likely to be those in moderately drought-stressed environments with high fertility (Huang et al. 2007). Soulé and Knapp (2006) argue that the effect of elevated CO<sub>2</sub> is evident in lower elevation ponderosa pine forests. Through tree ring analysis the authors show that ponderosa pine in the Pacific Northwest experienced increased growth since the 1950s that cannot readily be explained by precipitation and temperature. This growth increase is particularly evident in drought years, up to double the increase seen in wet years (Soulé and Knapp 2006). Other studies, however, emphasize precipitation and temperature as drivers of biomass change, even for relatively water-limited regions (Bunn et al. 2005; Jacoby and D'Arrigo 1997; Kienast and Luxmoore 1988). The variation in reported responses suggests that positive CO<sub>2</sub> fertilization effects on growth may often be overwhelmed by limitations in other resources.

An important trend to consider alongside productivity response is evidence of drought-related mortality and dieback events. Widespread increases in forest background mortality throughout the broader Western USA have been attributed to climate drivers rather than

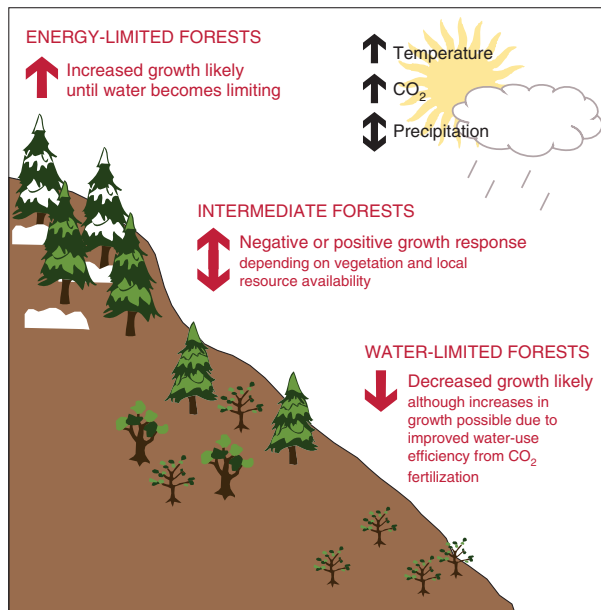


Fig. 3. Illustration of potential climate change impacts on vegetation gradients in temperate mountain environments.

increased competition (van Mantgem et al. 2009). Evidence of episodic drought-related forest dieback events have been reported in the Western USA and globally, in some cases, in areas not historically considered water-limited (Allen et al. 2010). Drought-stress effects on forests extend beyond first-order water deprivation to indirect effects such as increased fire frequency and higher potential for insect or disease outbreak. Westerling et al. (2006) report substantial evidence of increases in the frequency and magnitude of fires throughout forests in the Mountain West, with the largest increases occurring independent of land use change and instead likely linked to earlier timing of snowmelt in warmer years. There is also evidence of increased forest mortality due to insects and disease (Breshears et al. 2005; Hicke et al. 2006; Raffa et al. 2008). Disturbance regimes like fire and pathogen can shift quickly as a result of climate changes, in many cases overwhelming more gradual effects such as species composition or density changes (Dale et al. 2001).

In summary, there is growing evidence that forests, which comprise a significant proportion of vegetation water use for many Western US mountain watersheds, have changed in recent decades. Increased growth and biomass occur at high elevations and these changes might be expected to increase vegetation water use. Changes occurring in lower, more water-limited areas are more complex, with increases in growth/biomass in some cases and decreases in others. Increased frequency and severity of disturbances would likely reduce vegetation water use in the short term. Disturbances, however, can also provided opportunities for accelerated changes in composition and can lead to new species distributions with higher or lower water use (Hicks et al. 1991; West and Osier 1995).

#### *Translating Changes in Biomass into Changes in Streamflow*

Decades of research show a wide range of streamflow responses to changes in forest structure and composition (see reviews by Andréassian 2004; Bosch and Hewlett 1982; Brown

et al. 2005; Peel 2009). The effects of land management and disturbance on streamflow are often greater, and better studied, than potential changes in streamflow due to shifts in growth/productivity. Reviews of changes in water yield with reductions in forest cover show responses ranging from no change to increases of >500 mm in the first year following disturbance (Brown et al. 2005). Although most studies report that, in general, deforestation leads to short-term increases in annual runoff and afforestation/reforestation leads to decreases in the short term, longer-term and seasonal effects are highly variable due to site-specific factors such as vegetation type, precipitation, temperature, aspect, and location within the drainage system (Brown et al. 2005). Studies of changes in streamflow following disturbance in the Western USA show similar variability. For example, Mast and Clow (2008) found no substantial increases in runoff following deforestation from fire based on a paired catchment comparison for a small watershed in Glacier National Park. They argue that, in snowmelt-dominated systems, annual runoff increases following fire may be smaller than in rainfall-dominated systems. In snow-dominant mountains, spring snowmelt accounts for most of the runoff and, as snowmelt generally occurs when ET is low, the impact of vegetation water use may be small.

Changes in vegetation can also alter peak or flood flows. Literature on the impact of deforestation on peak flows focuses on more humid areas (such as the Pacific Northwest) where the impact of logging has received much attention. These studies suggest that impacts are greatest for smaller to intermediate storms (Jones and Grant 1996; Thomas and Megahan 1998). Recently, Wondzell and King (2003) examined increases in post-disturbance runoff following fire for a range of watersheds in the Western US mountains. They focus specifically on increases in flood flows associated with reduced infiltration capacity following fire. They conclude that if infiltration excess is not the dominant source of runoff, reduction in infiltration capacity associated with post-fire vegetation loss may not be important. The high infiltration capacity of soils in more humid portions of the Western USA means that, in these areas, increases in infiltration excess following fire may be negligible. So, for example, in the Pacific Northwest where rainfall is generally low intensity and soils are highly permeable, post-fire runoff increases may be mild. Increases, however, may be more substantial in the drier, interior Rocky Mountain region where infiltration decreases are compounded by significant summer high-intensity precipitation. In general, the sensitivity of peak flows to changes in vegetation structure depends strongly on the distribution of precipitation events, their intensity, and a priori soil and vegetation characteristics.

As discussed in the previous section, change in forest structure associated with warming may include growth-related increases in biomass at high elevations, increases or decreases in biomass at lower elevations, and composition shifts along elevational gradients. Impacts of these changes on streamflow may in many cases be smaller than those associated with land management or disturbance such as fire or disease, but their effects may be longer lasting. Shifts toward higher density ponderosa pine stands in the Western USA have been shown to decrease average soil moisture content (Zou et al. 2008). Using a coupled eco-hydrologic model, Tague et al. (2009) not only predict increases in leaf area for a high-elevation Sierra watershed under a warmer climate, but also show that these increases translate to less than a 5% decrease in total annual flow. Changes in vegetation with growth and biomass, however, can lead to changes in growing season water use and may amplify or buffer other climate-induced impacts on summer streamflow. For example, as discussed in the previous sections, climate warming can cause earlier spring snowmelt paired with increases in early-season biomass growth and therefore increased vegetation water use, magnifying snowmelt driven reductions in late-season summer



streamflow. Alternatively, drought-stress reductions in vegetation biomass could decrease vegetation water use and lessen reductions in summer streamflow associated with earlier snowmelt. The role vegetation plays in controlling summer streamflow is clearly evident in studies that show that the diurnal streamflow signal is dominated by vegetation ET (Lundquist and Cayan 2002). Furthermore, the strong seasonality of hydrographs in the Western USA means that summer streamflow is typically low, so small changes in volume can have critical consequences for aquatic ecosystems. Vegetation in riparian areas may be particularly important since these species are generally high water consumers and are opportunistically located within the water network to synchronize closely with stream and riparian groundwater levels (Rood et al. 2008). Hicks et al. (1991), for example, showed that a post-disturbance species shift in the riparian zone of a forested watershed in the Oregon Cascades led to 25% declines in summer baseflow.

### *Vegetation Controls on Snowmelt*

In addition to changes in the timing and magnitude of ET with consequences for streamflow, changes in vegetation structure can also alter snow accumulation and melt. There is a rich body of literature on the impacts of forest cover on local snow accumulation and melt, particularly related to interception and energy fluxes. Vegetation can significantly reduce snow accumulation through the sublimation of interception (Molotch et al. 2007; Montesi et al. 2004; Pomeroy and Schmidt 1993). However, vegetation also influences melt through effects on long wave radiation and the reduction of short wave radiation reaching under-canopy snow (Faria et al. 2000; Gelfan et al. 2004). There are ample field studies showing both of these effects, but their relative importance varies with canopy structure, radiation, temperature, and precipitation. For example, Veatch et al. (2009) investigated the impacts of vegetation on snow accumulation in New Mexico and showed that the greatest peak snow accumulation in this mountain environment occurs under intermediate (25–40%) canopy density due to an optimal balance of canopy controls on accumulation (throughfall increases with decreasing density) and ablation (melt decreases via snowpack shading with increasing density). At sites in New Mexico and the Colorado Rocky Mountains, Molotch et al. (2009) showed reduced snowmelt rates of up to 40% under canopy compared to open areas. Snow cover duration, however, was the same in under-canopy and open areas in New Mexico, whereas in Colorado snow cover depleted 9–15 days earlier under canopy. The authors suggest that the difference in canopy control between the two locations is due to an interaction between canopy structure (uniform versus ‘gappy’) and latitudinal controls on available solar radiation.

In addition to local effects, vegetation cover on neighboring landscapes can exert remote controls on snow dynamics. Rinehart et al. (2008) show that scattered radiation from forest canopy on surrounding hillsides can be an important control on snow accumulation and melt, particularly where vegetation cover is spatially or temporally variable. Interactions between topography, vegetation, and snowpack can be complex in these heterogeneous environments, but the energy exchange processes are reasonably well understood and therefore particularly suitable for model development and use. Overall, at both local and landscape scales, changes in snow accumulation and melt interact with changes in vegetation in interesting and dynamic ways. Vegetation water use, productivity, and stress are influenced by snow accumulation and melt, particularly in water-limited environments. At the same time, vegetation cover is an important control on snow dynamics, opening the door to potential positive or negative feedbacks between the two systems.

### *Species Composition and Streamflow*

Shifts in species composition are also expected under a changing climate, as species that flourish in warmer environments expand upward along elevational gradients, balances shift between co-located species, and invasive species better suited to the changed climate conditions expand opportunistically. Under a predictive biogeography model for the coterminous USA forced with an array of GCMs, Hansen et al. (2001) found that, under a warmer climate, encroaching forests overtake nearly all potential alpine habitats in the Western Mountains. Shrublands expand in the interior West, whereas grasslands expand in the arid Southwest. In the Southern Santa Rosa Mountains of California, Kelly and Goulden (2008) found that the average elevation of dominant plant species rose by 65 m over the past three decades and argue that these shifts are related to warming trends. As with changes in biomass, species shifts can affect local and downstream hydrology, in this case through depth of groundwater access, seasonality and magnitude of ET, surface changes such as modified infiltration capacity, and alteration of radiation and nutrient fluxes. In the case of both structural and compositional changes in vegetation, positive feedbacks between vegetation and hydrology may cause these downstream impacts to be long-lived. Net increases in ET and associated declines in water yield with woody plant encroachment have been shown to vary with climate, and are typically greater in humid and subhumid landscapes. Changes in water yield associated with species shifts in semi-arid areas, including those of the Southwestern US mountains, are highly variable and have been shown to depend on local geology, topography, and pattern of water input as rainfall and snowmelt (Huxman et al. 2005). Thus, in these regions, interactions between changing patterns of snow accumulation and melt, vegetation water use, and temperature with climate warming are likely to be particularly complex, and estimates of change will require integrated and site-specific assessments.

Even without changes in forest structure or composition, extended growing seasons under a warmer climate may also impact streamflow, certainly in seasonality of water flows if not in annual totals. Cayan et al. (2001) analyzed historical observations of first bloom of lilac and honeysuckle and snowmelt pulses in streamflow, and their findings from both independent datasets point to earlier spring onset across the Western USA since the mid-1970s. Timing of first bloom was linked to spring temperature anomalies, but independent of precipitation, and both the biological and hydrologic systems showed correlated responses. In areas where winter precipitation dominates, shifts in plant phenology to earlier 'greening' in deciduous species, earlier start to active photosynthesis in coniferous species, and earlier emergence for herbaceous and annual species may have significant impacts on water availability later in the growing season as soil water stores are exhausted.

### *Soil Decomposition and Vegetation Water Use*

For mountain environments, warmer temperature and changing snowpack dynamics also have the potential to alter soil biogeochemical cycling and nutrient availability (Meixner and Bales 2003; Trofymow et al. 2002) and potentially soil hydrologic properties (Hagedorn et al. 2010). Direct effects of increased temperature may be reinforced by changes in snow cover, although effects are complex. The presence of snow is not only linked to cooler temperature, but snow also acts to insulate underlying soil and reduce frost effects (Cécillon et al. 2010). In colder environments, warming soil temperatures typically increase rates of soil biogeochemical cycling and ultimately may

increase forest productivity when nutrients are limiting. If changes in soil composition enhance productivity, these changes may reinforce increased vegetation water use with warmer temperature (and lower runoff), particularly at high, more temperature-limited elevations.

### *Feedbacks to Climate*

Finally, analysis of ecohydrologic responses to climate warming must also consider feedbacks to the climate system itself. At a global scale, recent developments in GCM modeling emphasize the importance of including accurate representation of land-surface fluxes (Cao et al. 2009). In addition, short-term changes in ET under existing biomass and longer-term changes due to shifts in stand structure and composition may both influence the climate at more regional scales. Vegetation characteristics such as photosynthetic area, surface roughness, and albedo can alter climate variables such as temperature, humidity, wind speed, and precipitation at local and potentially regional scales. Cruz et al. (2010), for example, suggest that a relatively small ( $<1^{\circ}\text{C}$ ) increase in temperature during a 2002 warm, dry period in Australia's Murray–Darling Basin can be attributed to reductions in forest water use with increased water use efficiency. This study illustrates a relatively short-term response (e.g. prior to changes in stand structure/composition) and in a semi-arid system. In the Western USA, Stohlgren et al. (1998) found that crop irrigation in the Colorado plains altered climate in the adjacent Rocky Mountain slopes, as changes to energy and moisture fluxes between the land surface and atmosphere in the lower croplands caused changes to regional circulation patterns. In contrast to the Cruz study, Stohlgren also observed shifts in forest cover distribution in the adjacent mountains as a result of this climate feedback, indicating a longer-term response. Changes in vegetation water use efficiency in snow-dominated mountain regions may be either accelerated or moderated by warming temperature, given the complexity in surface environments and vegetation responses discussed in the preceding sections. Thus, for scenarios in which either the timing or magnitude of vegetation water use shifts, these climate feedbacks should be included in regional climate models.

### *Conclusion*

Globally, mountain environments provide over half the world's population with water (Bandyopadhyay et al. 1997; Viviroli et al. 2007). Mountain regions also support a broad ecological diversity and a significant proportion of protected natural area (Beniston 2003). Thus, ecohydrologic responses of mountain systems to warming will continue to be a research area of critical importance. Our review of recent literature shows a complex set of responses that vary over space and time. Figure 4 presents a road map that summarizes the main components of ecohydrologic responses to climate change considered in our review. As this figure illustrates, there may be a cascading set of responses; for example, earlier snowmelt driven changes in soil hydrology can lead to short-term changes in water availability for runoff and vegetation, and ultimately changes to stand structure and long-term water use. Which processes and response are most important likely depends on scale and specific location of interest. Clearly changes in snow accumulation and melt are important drivers of hydro-ecologic response in mountain environments and the magnitude of changes in snow dynamics varies with location and degree of climate change. From a vegetation water use perspective, responses also differ between temperature-limited and water-limited regions; for mountain ranges at continental and global scales,

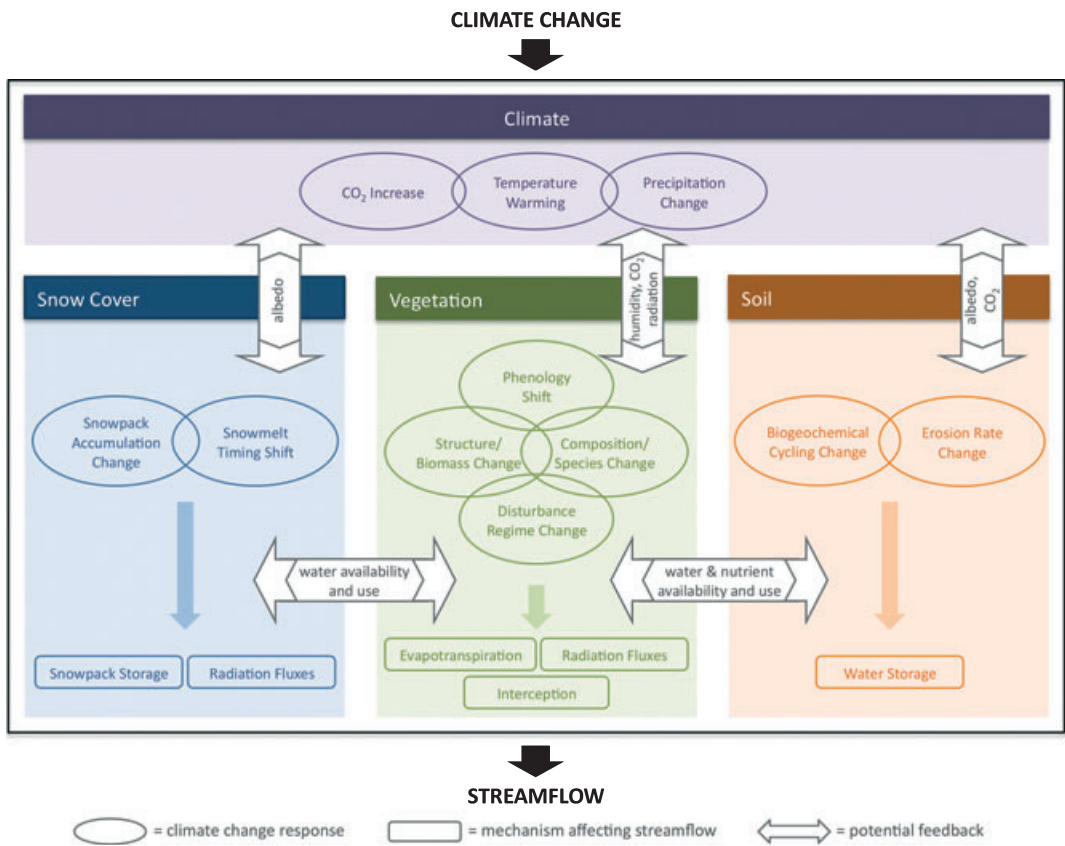


Fig. 4. Schematic of potential mechanisms of and feedbacks between ecohydrologic responses to climate change.

which factor is growth-limiting varies along elevation and latitudinal gradients. In the Western USA, response differences between interior locations that receive substantial summer precipitation and those that do not are likely to be important. Disturbances also play a key role in controlling the magnitude and timing of responses, and are perhaps the most challenging to model. Within this overarching framework of scale, location, and disturbance, however, there is still a need to increase our understanding of local vegetation responses to climate change and how these responses might affect the timing and magnitude of vegetation water use. Some of the greatest uncertainties are in understanding how climate-driven changes in vegetation water use may alter streamflow regimes. It may not be clear, for example, to what degree riparian vegetation water use may be vulnerable to warming and how changes in riparian vegetation may influence summer streamflow.

Given these uncertainties, recent initiatives focused on the intensive study of coupled eco-hydrologic processes in mountain environments are critical. In particular, studies are needed to direct monitoring, analysis, and modeling to examine how changes in vegetation water use are mediated by plant physiology, community structure, and also by inputs from and feedbacks to the hydrology of the system. Several recent multi-investigator initiatives in the Western USA are designed to address these questions. The Western Mountain Initiative (<http://www.westernmountains.org/>) uses a network of sites and an

interdisciplinary team to explore the effects of climate change on the coupled hydro-ecological responses that determine vulnerability of Western Mountain ecosystems to change. The US National Science Foundation has established three Critical Zone Observatories within the Western US mountains ([http://www.czen.org/sites/us\\_czo](http://www.czen.org/sites/us_czo)). These observatories serve as new long-term monitoring sites specifically focused on linking together a broad suite of measurements of coupled soil–atmosphere–vegetation systems. The Consortium for Integrated Climate Research on Western Mountains (CIRMOUNT, <http://www.fs.fed.us/psw/cirmount/>) is a network of researchers that supports collaborative scientific research and synthesis. Although CIRMOUNT focuses on western North America, the organization partners globally with the international Mountain Research Initiative (<http://mri.scnatweb.ch/>). These observation and research synthesis networks all demonstrate a strong focus on ecohydrology and will likely provide new insights into the mechanisms through which vegetation water use, the physical hydrologic system, and climate interact.

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### *Short Biographies*

Dr Christina Tague received her PhD from the Department of Geography at the University of Toronto, Canada, and has an undergraduate degree from the Department of Systems Design Engineering at the University of Waterloo, Canada. Dr Tague investigates climate and landuse/land cover change impacts on streamflow regimes and watershed biogeochemical cycling, emphasizing the interactions between hydrology and ecosystem processes. She specializes in the development and application of spatial models. Her work seeks to design models as a flexible, adaptive framework for integrating conceptual understanding with data from a variety of sources, including intensive field-based monitoring and experimentation and remote sensing. Dr Tague is one of the principle developers of RHESSys, Regional Hydro–Ecologic Simulation System, a modeling framework that provides science-based information on the spatial patterns of vulnerability in water quantity and quality, and ecosystem health. Current projects include modeling climate change impacts on snowpack and summer streamflow patterns in the mountains of the Western USA, and examining how urbanization alters drainage patterns and associated biogeochemical cycling at part of the Baltimore Long Term Ecological Research Site and in selected Southern California watersheds.

Aubrey L. Dugger is currently pursuing a PhD in hydrology at the Bren School of Environmental Science and Management at the University of California, Santa Barbara. She received a Master of Science in Civil and Environmental Engineering from the University of Texas at Austin and a Bachelor of Science in Civil Engineering from Duke University. Aubrey's prior academic and professional work focused on the synthesis of hydrological modeling and geospatial analysis tools, with applications ranging from flood prediction and storm water management to habitat restoration. Her current research explores the interacting effects of climate and land use changes on semi-arid mountain watersheds with the ultimate goal of improving impact assessment on downstream water supply systems.



## Note

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