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Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses

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ABSTRACT

Widespread, rapid, drought-, and infestation-triggered tree mortality is emerging as a phenomenon affecting forests globally and may be linked to increasing temperatures and drought frequency and severity. The ecohydrological consequences of forest die-off have been little studied and remain highly uncertain. To explore this knowledge gap, we apply the extensive literature on the ecohydrological effects of tree harvest in combination with the limited existing die-off ecohydrology research to develop new, relevant hypotheses. Tree mortality results in loss of canopy cover, which directly alters evaporation, transpiration, and canopy interception and indirectly alters other watershed hydrologic processes, including infiltration, runoff, groundwater recharge, and streamflow. Both die-off and harvest research suggest that for most forests, water yield can be expected to increase following substantial loss of tree cover by die-off. We hypothesize that where annual precipitation exceeds ~500 mm or water yield is dominated by snowmelt, watersheds will experience significantly decreased evapotranspiration and increased flows if absolute canopy cover loss from die-off exceeds 20%. However, recent observations suggest that water yield following die-off can potentially decrease rather than increase in drier forests. To reliably predict die-off responses, more research is needed to test these hypotheses, including observations of multiple water budget components and the persistence of ecohydrological effects with the post-die-off successional dynamics of tree recruitment, understorey growth, and interactions with additional disturbances. With die-off, mitigation and restoration options are limited and costly, necessitating societal adaptation; therefore, die-off ecohydrology should be a high priority for future research. Published in 2011. This article is a US Government work and is in the public domain in the USA.

KEY WORDS ecohydrology; die-off; tree mortality; forest mortality; evapotranspiration; recharge; water yield; bark beetle; tree pests

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INTRODUCTION

Global climate change is projected to directly alter the hydrological cycle through changes in precipitation and temperature (IPCC, 2007). In addition, if such climate changes are sufficient to trigger changes in vegetation, as expected, additional potentially important hydrological changes to water budgets will occur (Troch *et al.*, 2009). Ecohydrology research assessing such feedbacks between hydrological and ecological aspects is a current pressing challenge, particularly if rapid and large-scale changes in vegetation are triggered (Jackson *et al.*, 2009; Wilcox 2010). An emerging picture of global change ecology suggests that the nature and pace of climate-driven vegetation adjustments can be rapid and abrupt (Allen and Breshears, 1998; Overpeck and Cole, 2006; Backlund *et al.*, 2008).

Of particular concern is the potential for changes in climate to trigger rapid and widespread vegetation die-off through tree mortality due to a combination of drought, warmer temperatures, and/or infestation by pathogen and/or pests (Allen *et al.*, 2010). A recent global assessment of tree die-off over the past 30 years on all six forested continents suggests that climate-driven forest die-off may be emerging as a global phenomenon (Allen *et al.*, 2010). Several recently documented die-offs were extensive in scale, for example, affecting 130 000 km^2 of pine (*Pinus* spp.) forests in western Canada by the end of 2006, 55 000 km^2 of Australian eucalypts (*Eucalyptus* spp.) by the late 1990s, and over 600 000 km^2 in total of non-contiguous coniferous forests in western North America in the last decade (Fensham and Holman, 1999; Kurz *et al.*, 2008; Bentz *et al.*, 2009; Fensham *et al.*, 2009; Allen *et al.*, 2010).

Patterns of mortality are often linked to the interaction between climate conditions and pest dynamics. Precipitation variability can have both direct effects on vegetation

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growth and survival as well as predisposing forests to pest outbreaks (McDowell *et al.*, 2008; Raffa *et al.*, 2008; Allen *et al.*, 2010). Projected trends in precipitation portend substantial poleward shifts in storm tracks that will decrease mean precipitation at mid-latitudes as well as increased temporal precipitation variability (Easterling *et al.*, 2000; IPCC, 2007; Milly *et al.*, 2008). Significant increases in drought severity and frequency have been observed in association with even minor trends in mean precipitation (Luce and Holden, 2009), and these can have important consequences for die-off vulnerability. Warmer temperatures amplify drought effects, weaken trees, and reduce their defenses, while simultaneously facilitating increased populations of tree pests (Breshears *et al.*, 2005; Stahl *et al.*, 2006; McDowell *et al.*, 2008; Raffa *et al.*, 2008; Worrall *et al.*, 2008; Allen *et al.*, 2010), and likely increase mortality even without accounting for associated changes in precipitation variability (Adams *et al.*, 2009). Tree mortality can occur along a progression of severity, from subtle increases in background mortality (e.g., van Mantgem *et al.*, 2009), to affecting only a single species in a diverse forest (e.g., through a host-specific tree pest; MacDonald and Hoff, 2001; Ellison *et al.*, 2005; Ford and Vose, 2007), and, of particular concern ecohydrologically, die-off of a high percentage of individuals in forests dominated by a few tree species (e.g., Fensham *et al.*, 2003; Breshears *et al.*, 2005; Kurz *et al.*, 2008).

The ecohydrological consequences of forest die-off have not been widely studied and remain highly uncertain. Despite recent projections of the importance of die-off (Allen *et al.*, 2010) and its potential to impact ecohydrological processes, assessments of ecohydrological consequences of drought- and infestation-triggered tree die-off and associated research priorities are lacking. However, a few studies do exist, and relevant insights can be obtained from studies of ecohydrological responses to other types of forest disturbance. To explore this knowledge gap and develop relevant hypotheses about the potential ecohydrological consequences of die-off, we consider the extensive literature on the ecohydrological effects of disturbances that reduced tree cover in combination with the limited existing die-off ecohydrology research. More specifically, we (1) review the limited literature on tree die-off hydrological effects and link it to the much larger body of work on responses to harvest (after determining that responses following fire are much less relevant); (2) consider the direct and indirect ecohydrological effects of tree die-off; (3) compare short- and long-term potential ecohydrological responses to die-off; (4) examine applications and implications for forest management; and (5) identify related research hypotheses and priorities. Regarding our overall approach, an important aspect of ecohydrology is the partitioning of the water budget among relevant components (Newman *et al.*, 2006), which are often lumped together, particularly with respect to components of evapotranspiration (Savenije, 2004). To be explicit about the components—soil evaporation (E), plant transpiration (T), and evaporation of water intercepted by the plant canopy (I)—we refer them either individually, collectively as ETI, or as ET when we are referring to the total of only E and T without accounting for I.

COMPARING CHARACTERISTICS OF TREE MORTALITY BY DIE-OFF TO HARVEST AND FIRE

We first begin by comparing the general characteristics of changes from die-off to the changes associated with tree removal by harvest and fire. Here, we refer to harvest as externally applied tree removal that includes multiple felling methods, cabling, scraping, and/or herbicide application; and fire as burning substantial enough to remove overstorey canopy cover. The primary effect of die-off is a loss of tree canopy cover that reduces T and I by the overstorey. Tree canopy cover loss is also a dominant effect of forest harvest and fire, so hydrological responses to these forest manipulations could provide useful insights into the hydrological consequences of die-off. Moreover, extensive literature exists on the ecohydrological consequences of tree harvest and fire (e.g. Stednick, 1996; Andréassian, 2004; Brown *et al.*, 2005; Shakesby and Doerr, 2006; Montes-Helu *et al.*, 2009).

Although die-off, harvest, and fire all result in overstorey canopy cover reduction, important distinctions exist among their effects on other ecohydrological characteristics (Table I). For example, in contrast to some types of forest harvesting practices (e.g., complete clear cuts with no residual seed trees) and to much high-severity, stand-replacing wildfire, in most documented tree die-off events the mortality is not continuous across the landscape and rarely results in complete conversion to

Table I. A comparison of effects relevant to hydrological processes for three disturbance types: die-off, harvest, and fire.

Associated changes	Presence of change with disturbance type		
	Die-off	Harvest	Fire
Canopy cover loss	X	X	X
Soil compaction (from roads and skid trails)		X	
Standing snags remain	X		X
Heated-soil water repellency			X
Litter layer/understorey burning			X

Canopy cover loss is common to all three, but fire causes more changes relevant to hydrological processes, suggesting that the potential hydrological consequences of die-off have more in common with those of harvest than for fire.

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non-forest (Allen *et al*., 2010). An important distinction between harvest and die-off is that harvesting has effects associated with the building and use of roads and skid trails required to remove timber. Decreased infiltration on compacted surfaces can increase overland flow affecting both water yield and peak flows at the watershed level (Jones and Grant, 1996; Luce, 2002; Wemple and Jones, 2003; Hubbart *et al*., 2007).

Although fire can certainly reduce overstorey tree canopy cover, its reported ecohydrological effects make fire less similar to die-off than harvest. Unlike harvest and die-off, fire abruptly alters ground surface cover, by consuming the litter layer and understorey vegetation. Fire can also create soil water repellency when soil heating vaporizes organic material, which condenses and bonds with cooler, underlying mineral soils (Table I, DeBano, 2000; Lewis *et al*., 2006; Shakesby and Doerr, 2006; Lane *et al*., 2010). Immediately after fires, T and I diminish due to the lack of overstorey and understorey canopy, but increased exposure of bare soil and dark charred surfaces likely results in increased E. Increases in overland flow due to combinations of water repellency and loss of soil organic horizons can drive substantial rill formation and erosion, including debris flows that transport sediment and alter stream channel morphology while reducing soil infiltration (Istanbulluoglu *et al*., 2002, 2003; Cannon *et al*., 2009; Moody and Martin, 2009). Low severity fires rarely yield such dramatic outcomes, but also commonly result only in understorey biomass consumption and some mortality of smaller trees, differing from die-off for which mostly larger canopy elements are killed and understorey plants are potentially released for increased growth (Klenner and Arsenault, 2009).

Although both die-off and fire leave dead standing snags while harvest does not, harvest has more effects in common with die-off relevant to hydrological process than does fire (Table I). Die-off effects on forest structure often resemble a 'thinning-from-above' harvesting treatment, where larger trees are selectively removed from the stand, since larger trees are often more likely to be killed during die-off (Mueller *et al*., 2005; Floyd *et al*., 2009; Klenner and Aresenault, 2009) if the drought effects are not completely overwhelming with respect to tree size/age. Ideally, a consideration of the ecohydrological consequences of tree die-off should be entirely based on die-off results. However, the limited literature on die-off ecohydrology and the very extensive literature on forest harvesting hydrology together necessitate considering both to hypothesize consequences of tree die-off broadly across different forest types. Therefore, we will draw on both harvest and die-off literature to explore the ecohydrological consequences of die-off in the following sections, while keeping in mind that die-off is distinct from harvest in some effects (we will not consider fire effects further). Key lessons from studies of the ecohydrological effects of harvest are that both the intensity of the initial disturbance and the successional pathways after disturbance affect the magnitude of changes, and their persistence (Stednick, 1996; Brown *et al*., 2005).

THE EFFECTS OF TREE MORTALITY

We next review the limited available literature on ecohydrological responses to drought- and infestation-induced die-off and evaluate it in the context of direct effects, indirect effects, and persistence of effects. We relate each section to relevant literature on harvest (but not fire, as addressed in the previous section), as well as to more general water budget research. The published research on ecohydrological responses to drought- and infestation-triggered tree die-off is relatively limited and is currently restricted to mortality of conifer species, mostly in western North American watersheds (Table II). Much of the recent research has been conducted in response to two regionally extensive forest mortality events: piñon pine (*Pinus edulis*) die-off in the southwestern US (Breshears *et al*., 2005) and lodgepole pine (*Pinus contorta*) die-off in western Canada (e.g. Kurz *et al*., 2008). Studies include empirical and modelling assessment of the effects of tree mortality on ETI, snow ablation and accumulation, peak flow, and water yield (Table II). Among this small group of studies, mostly with similar forest cover types, responses vary considerably, preventing the crafting of well-supported, broadly applicable conclusions on the hydrological effects of die-off. Nonetheless, the studies do provide important insights that help frame relevant hypotheses and future research priorities. To consider the ecohydrological effects of tree mortality, we begin with direct effects, specifically the ETI consequences of tree cover loss and then consider indirect effects associated with the results of ETI change on other water balance components.

Direct effects

Die-off direct effects. The direct ecohydrological effects of tree die-off relate to changes in canopy and ground cover, which exert important influences on many ecosystem processes (Breshears, 2006). Tree canopy cover plays an important role in regulating ETI through opposing influences from its E, T, and I components. Decreased canopy cover reduces overstorey T and I, a negative feedback on overall ETI (Figure 1). Yet at the same time, canopy cover loss increases the wind and solar energy reaching the land surface, which drives bare soil E and understorey T, a positive feedback on ETI. The balance of these competing E, T, and I responses to canopy cover reduction ultimately determines the extent of direct tree die-off effects on overall ETI. Studies that partition ETI into these components, at both canopy and near-surface levels, are needed to better understand these opposing effects on die-off hydrology (Savenije *et al*., 2004; Newman *et al*., 2006; Spittlehouse 2007; Wang *et al*., 2010).

Table II. A summary of research on the hydrological effects of tree die-off.

Location	Ecosystem type	Species affected	Component studied	Effect of mortality	References
Arizona, USA	Conifer forest and woodland	*Pinus edulis, Pinus ponderosa*	Near-ground energy	Increased near-ground energy and potential surface ET	Royer *et al.* (2010, 2011)
British Columbia, Canada	Conifer forest	*Pinus contorta*	ETI, drainage	Decreased ETI, increased drainage	Spittlehouse (2007), Redding *et al.* (2008)
British Columbia, Canada	Conifer forest	*P. contorta*	Snow accumulation and ablation	Increased snow accumulation and ablation	Boon (2007, 2009)
British Columbia, Canada	Conifer forest	*P. contorta*	Snow surface albedo	Decreased albedo, increased snow loss	Winkler *et al.* (2010)
British Columbia, Canada	Conifer forest	*P. contorta*	ETI, water yield, snowmelt peak flow	Increased streamflow	Carver *et al.* (2009a, 2009b), Weiler *et al.* (2009)
Colorado, USA	Conifer forest	*Picea engelmannii*	Water yield	Increased streamflow	Bethlahmy (1974, 1975)
Colorado, USA	Conifer forest	*P. contorta, Abies lasiocarpa*	Water yield	Unchanged and decreased streamflow	Somor (2010)
Colorado, USA	Conifer forest	*P. contorta*	Soil and stream chemistry	Increased soil N, NO_3, NH_4, unchanged stream NO_3	Clow *et al.*, (2011)
Germany	Mixed hardwood/conifer forest	*Picea abies*	Water yield, groundwater, runoff, NO_3 concentration	Increased streamflow, groundwater recharge, runoff, and NO_3 concentration	Beudert *et al.* (2007)
Montana, USA	Conifer forest	*P. contorta*	Water yield	Increased streamflow	Potts (1984)
North Carolina, USA	Mixed hardwood/conifer forest	*Tsuga canadensis*	Transpiration	Reduced spring and winter stand transpiration	Ford and Vose (2007)
Southwest (AZ, CO, NM, UT) USA	Conifer woodland/savanna	*P. edulis*	Water yield	Decreased streamflow	Guardiola-Claramonte (2009), Guardiola-Claramonte *et al.* (In press)

Studies include modelling and empirical assessments of energy budgets, overstorey transpiration and interception, snow dynamics, water yield, groundwater recharge, runoff and NO_3 concentration responses. Nearly all studies are for North American ecosystems and watersheds (mostly western North America) where evergreen conifer species experienced substantial climate-related mortality, often associated with insect pests.

Few published studies have directly considered ETI changes following tree mortality (Table II). In the southern Appalachian Mountains of the United States, recent eastern hemlock (*Tsuga canadensis*) mortality was caused by an infestation of the host-specific hemlock woody adelgid (*Adelges tsugae*), a phloem-consuming insect (Ford and Vose, 2007). This affected hemlock species, an evergreen conifer, transpires year round, even while the dominant hardwood species are inactive in the winter, giving it a unique role in that forest ecosystem. Ford and Vose (2007) estimated that the loss of this species from the forest would initially reduce annual overstorey T by 10% and spring T by 30%. In British Columbia, an assessment of water balance for a forested lodgepole pine watershed suggested that infestation-induced tree mortality reduced overall ETI, by

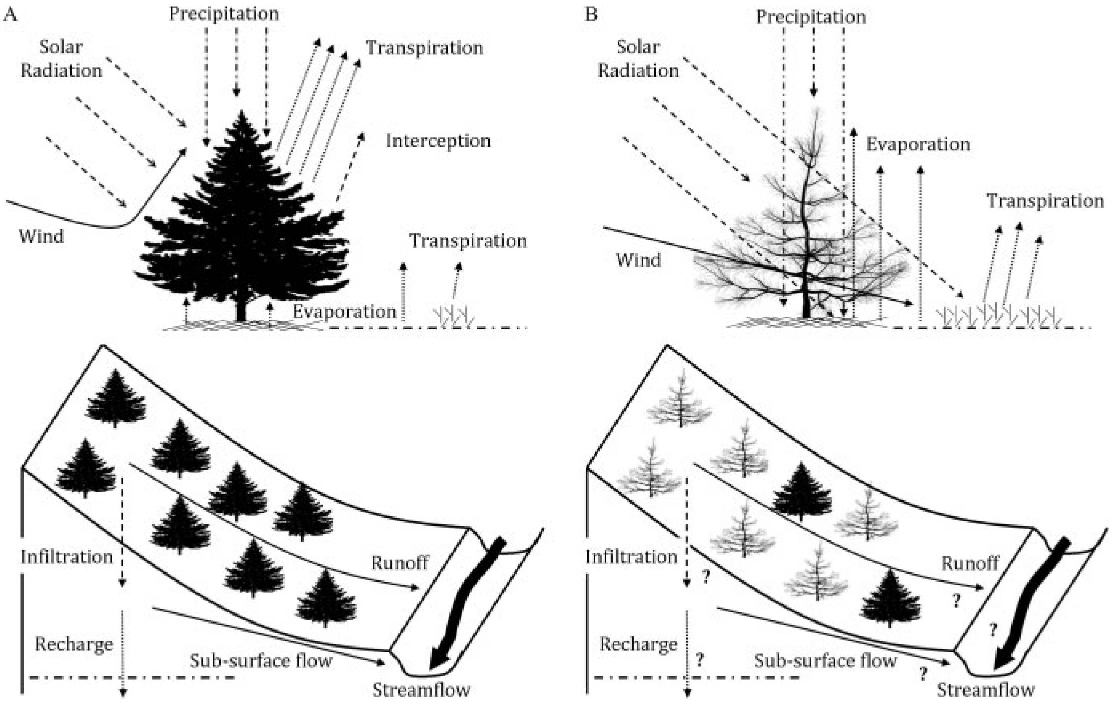

Figure 1. The relative effects of canopy cover on water budget components at the patch and hillslope scale under normal conditions (A) and after die-off (B). Live trees transpire soil water and block solar radiation, wind, and precipitation from reaching the soil surface. After tree mortality, more solar radiation, wind, and precipitation reaches the surface as interception is greatly reduced; overstorey transpiration decreases greatly; understorey transpiration increases; and evaporation at the surface is increased. The interactions among all of these tree-cover-related evapotranspiration factors determine the net direct effects of canopy cover reductions on infiltration, runoff, groundwater recharge, subsurface flows, and streamflow.

approximately 50% (Spittlehouse, 2007; Redding *et al.*, 2008). In two northern Arizona ecosystems, tree die-off increased near-ground energy inputs that drive near-ground surface ET (understorey T and bare soil E only, not overstorey T or I) by 12% for piñon pine and 19% for ponderosa pine (Royer *et al.*, 2010, 2011). These increases in near-ground energy depended on pre-mortality canopy cover and were greatest at intermediate canopy cover.

Snow I and ground snowpack accumulation are highly dependent on canopy cover, so tree mortality can exert a strong influence on the hydrology of snowmelt-dominated watersheds (Boon, 2007, 2009, 2011; Redding *et al.*, 2008). Storage of intercepted snowfall by tree canopies varies with branch and snow characteristics, but can be an order of magnitude greater (in water equivalent) than canopy storage of rainfall (for non-die-off effects, see Lundberg and Halldin, 2001). Because sublimation of intercepted snowfall is also greater than that of snowpack on the ground, tree canopies can block a significant portion of precipitation from reaching the land surface when it falls as snow (Boon, 2007, 2009, 2011; Redding *et al.*, 2008). Canopy cover declines associated with tree mortality result in greater snow throughfall to the ground, while also allowing increased solar energy inputs to melt snow compared to areas with undiminished canopy cover (Boon, 2007, 2009, 2011).

The broad regional extent of the ongoing conifer die-off associated with a massive mountain pine beetle (*Dendroctonus ponderosae*) outbreak in British Columbia, a region with snowmelt-dominated hydrology, has spurred a number of studies into the effects of die-off on snow processes and hydrology, many of which are still ongoing (Winkler and Boon, 2010). Results from recent studies showed that ablation rate (the sum of E and sublimation) of ground snowpack was only slightly elevated for beetle-killed stands relative to live stands, and the snow accumulation in beetle-killed stands resembled that in clear-cut and treeless areas, except in years when high snowfall overwhelmed the canopy interception of live stands (Boon, 2007, 2009, 2011). Snowpack persisted longest in living stands, indicating that tree mortality can trigger earlier, intensified snow losses as continued needle loss causes dead stands to resemble cleared areas with time. At several sites, litterfall from dead conifers landing directly onto snowpack reduced surface albedo and increased ablation and melt (Winkler *et al.*, 2010). A small amount of litter on the snow surface had a large, nonlinear effect, causing snowpack loss that was similar to that for an open area. Results of research on the response of snow dynamics to pine beetle mortality in Colorado, USA, are consistent with work in British Columbia, showing increased accumulation and faster snowpack loss in affected stands (Pugh and Small 2011).

Other relevant research on direct effects. Regarding other relevant research on snow, the reported changes in snow dynamics following die-off are consistent with snow interception and snowpack responses to harvest, including snowmelt timing (Wilm, 1944; Troendle and King, 1985; Berris and Harr, 1987; Jost *et al.*, 2007), and their associated responses to amount of canopy cover (Molotch *et al.*, 2009; Veatch *et al.*, 2009). Canopy cover reduction by harvest can lead to earlier, faster, and more synchronous snowmelt (Jones, 2000; Tonina *et al.*, 2008). Lacking from die-off studies, however, is research on the partitioning of ETI, which has been studied in the context of other changes or variation in canopy cover. Studies that have addressed canopy cover reductions due to factors other than die-off on ET partitioning and overall ETI demonstrate the potentially opposing influences of E, T, and I components. In thinned and unthinned semi-arid ponderosa pine (*Pinus ponderosa*) stands in northern Arizona, assessment of ET partitioning indicated that an 82% reduction in basal area (45% reduction in leaf area index) increased E and ET overall during a dry summer, when the T component was small due to low tree stomatal conductance (Simonin *et al.*, 2007). However, during the following wet spring when tree stomatal conductance was high, overall ET was higher for the unthinned treatment when the T component dominated ET. A study of semi-arid mesquite (*Prosopis chilensis*) trees, in an experimental manipulation that varied canopy cover to multiple levels in a large controlled-environment glasshouse, showed that overall ET rose with increased canopy cover, as a result of increasing T exceeding the corresponding reduction in E (Wang *et al.*, 2010). Although I is highly dependent on rainfall event size, canopy storage capacity is thought to increase linearly with canopy cover (Gash 1979; Gash *et al.*, 1995; Valente *et al.*, 1997). Thinning of a Mediterranean oak (*Quercus ilex*) stand with a reduction of tree basal area by 33% caused a decrease of 34% in I at an experimental forest in southern France (Limousin *et al.*, 2008). However, increased I does not always equate with increased moisture loss to the atmosphere. Particularly for forests where cloud and fog interception are important moisture inputs, throughfall can exceed precipitation, and canopy loss could decrease moisture reaching the ground (Harr, 1982; Brauman *et al.*, 2010).

Indirect effects

Die-off indirect effects. Direct hydrological consequences of tree mortality include changes in E, T, I, and snow accumulation and melt dynamics. Considering these changes to the water balance, tree mortality may indirectly affect other aspects of hydrological functioning, such as infiltration and flow path partitioning, which would subsequently result in changes in soil moisture status, groundwater recharge dynamics, and streamflow volume and timing. For example, if tree mortality decreases overall ETI, as discussed above, and precipitation remains the same, then more water is available for these other components as an indirect effect of tree die-off. Whether this water enters the soil or becomes overland flow will depend on the infiltration capacity of the soil, which could be increased through inputs of dead material like needle litter from dying trees and creation of macropores when dead trees fall, or decreased if soil organic material is washed away following tree mortality.

Subsurface connections such as fractured bedrock that create flow paths to groundwater are not directly affected by tree mortality (although there could be potential effects from roots in rock; Schwinning, 2010), yet affect whether water that enters the soil following tree mortality will contribute to groundwater recharge (for non-die-off effects, see Wilcox, 2002; Seyfried and Wilcox, 2006; Wilcox *et al.*, 2006, Wilcox and Huang, 2010). Published studies on the indirect effects of tree mortality on flow path partitioning are rare, and assessments of groundwater recharge from die-off are almost non-existent. At one intensively studied experimental watershed in southern Germany, Grosse Ohe, an isotopic tracer model was used to partition discharge response for a catchment that underwent a $\sim$53% forest cover loss though Norway spruce (*Picea abies*) mortality (Beudert *et al.*, 2007). Tree mortality caused a 39% decrease in ET associated with a 135% increase in runoff and a 125% increase in groundwater flow. Additionally, NO_3 concentrations of soil water increased from 10 to 200 mg/l at 40 cm in depth and to 130 mg/l at 100 cm, demonstrating that tree die-off can affect water quality. In a watershed in Colorado experiencing extensive mortality of lodgepole pine NO_3, NH_4, and total N increased in soils under stands of dead trees, but this did not translate to elevated NO_3 in stream water in the near-term following die-off (Clow *et al.*, 2011).

Increased groundwater recharge can translate to increased streamflow volumes and higher flows during low flow periods, and in areas where the water table is already close to the ground surface, it may increase the potential for saturation excess overland flow or unfavourable conditions for seedling establishment and tree growth. This combination of higher antecedent wetness conditions, elevated groundwater levels, and more area available for overland flow generation could lead to changes in the timing and magnitude of responses to rainfall and snowmelt. Streamflow, which integrates overland, subsurface, and groundwater flows differently depending on watershed properties, may ultimately be indirectly affected by tree mortality. Quantified as water yield, streamflow will increase if tree mortality decreases watershed ETI, and conversely decrease if ETI is increased.

The variation in water yield responses reported for die-off ecohydrology studies, all in watersheds with conifer mortality involving bark beetle outbreaks, demonstrates a wide range of possible hydrological responses to tree die-off (Table II). In two northern Colorado river drainages in the United States annual water yield increased by 10% following a bark beetle outbreak that killed up to 80% of trees in the late 1930s and early 1940s, mostly from nonproportional streamflow increases during wet years (Bethlahmy, 1974, 1975). At Jack Creek in southern Montana, United States, a mountain pine beetle outbreak killed 35% of trees across the watershed from 1975 to 1977 (Potts, 1984). This event caused a 15% increase in annual water yield, a 2–3 week advance in the onset of snowmelt-driven flows, and a 10% increase in low flows over a period of 5 years post-mortality. The research in southern Germany at Gross Ohe showed that peak flows in a catchment with ~53% tree mortality increased by a factor of 2·2 relative to an adjacent catchment mostly unaffected by die-off (Beudert *et al.*, 2007).

In contrast, research examining the streamflow response to mortality of lodgepole pine and subalpine fir (*Abies lasiocarpa*) in eight Colorado, US catchments found that streamflow relative to precipitation was unchanged in seven catchments where canopy cover loss averaged 43%, and even decreased by 31% in one catchment that had 50% tree mortality (Somor, 2010; unpublished manuscript). In addition, an assessment of water yield changes in the southwestern United States after extensive piñon pine die-off found that five semi-arid basins, ranging in size from ~1000 to ~5000 km^2 and which lost 11–21% of tree cover, had on average ~50% less water yield post-mortality after correcting for precipitation changes (Guardiola-Claramonte, 2009; Guardiola-Claramonte *et al.*, in press). In addition, these basins had significantly delayed streamflow generation compared to similar unaffected basins. The responses of these watersheds were attributed to rapid post-die-off understorey growth detected in a remote sensing analysis for the same basins (Rich *et al.*, 2008). This increase in understorey cover was speculated to have reduced overland flow (consistent with Zou *et al.*, 2010) and increased infiltration, T, and I, increasing overall ETI in these dry, low-elevation watersheds (Guardiola-Claramonte, 2009; Guardiola-Claramonte *et al.*, in press).

The extensive mountain pine beetle outbreak across British Columbia, Canada in the last decade has driven development of a process-based hydrological model to estimate peak- and low-flow responses across the mostly ungauged Fraser River Basin (Carver *et al.*, 2009a,b; Weiler *et al.*, 2009). Incorporating changes in ETI and snow dynamics with flow components and discharge responses, the model suggests that with complete mortality of all trees in the watershed, snowmelt-induced peak flows increase with area of forest affected, up to a maximum of 140%, with a 26% increase predicted at the Fraser River outlet. High variability in these projections across the basin revealed potential nonlinear thresholds in the hydrological response and specific effects of differences in runoff generation processes (i.e., Hortonian overland flow, saturation excess overland flow, subsurface flow) among the watersheds with increasing mortality.

Other relevant research on indirect effects. As noted previously, the wide range of responses documented in the small set of die-off hydrology literature calls for drawing on the forest harvest literature to further consider likely indirect effects of forest die-off. Early reviews of paired catchment studies in US watersheds found harvest responses to be highly variable (Bosch and Hewlett, 1982). However, more recent reviews have focused on organizing responses by climate and treatment characteristics (e.g. Brown *et al.*, 2005). Harvesting intensity is a primary determinant of water yield response, with canopy cover removal thresholds of 20–25% suggested to enable statistical detection of a response across several environments (Bosch and Hewlett, 1982; Stednick, 1996; Brown *et al.*, 2005; Troendle *et al.*, 2010). However, for cases with a reduction of less than 20% forest cover, lack of significant hydrological responses could be due to low statistical power from short post-treatment records or the effects of different harvesting techniques (McMinn and Hewlett, 1975).

Locations with greater annual precipitation tend to show greater hydrological sensitivity to forest treatments compared to drier locales (Bosch and Hewlett, 1982; Stednick, 1996; Troendle *et al.*, 2010). Similarly, results from high elevation lodgepole pine forest also show that at a given site, water yield in wetter years is more sensitive to harvest (Troendle and King, 1987). A global analysis of catchment studies comparing the ET of forested versus non-forested watersheds with similar climates demonstrated that potential water yield changes could be predicted from annual precipitation (Zhang *et al.*, 2001). This assessment suggested that little change should be expected with a shift from forest to grassland for sites below 500 mm of annual rainfall because potential ET at these sites is a large proportion of precipitation. The largest increases in water yield

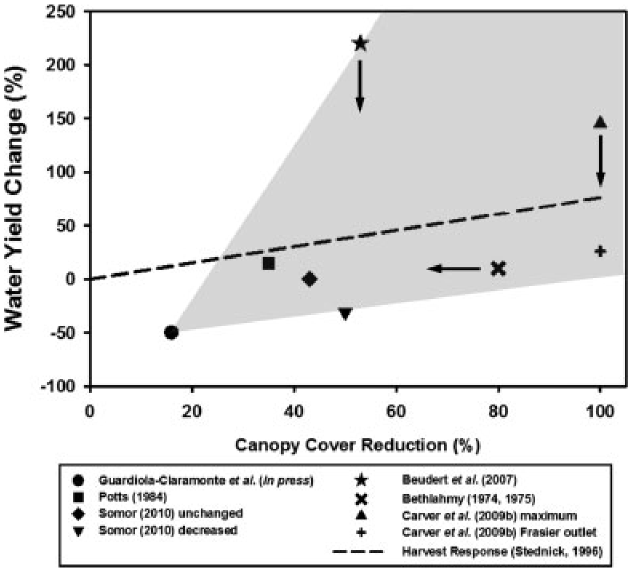

Figure 2. The relationship between canopy cover reduction and annual water yield change for die-off hydrology studies that measured or estimated water yield. Points represent individual studies from Table II. For Somor (2010) the response of seven catchments where water yield was unchanged (diamond) and the single catchment with decreased flows (triangle pointing down) are shown separately. Values shown for Carver *et al.* (2009b) are modelled peak flow maximum (triangle) and Frasier River outlet peak flow changes (plus sign). The grey area represents the range of hypothesized water yield responses to die-off. Arrows indicate that for Beudert *et al.* (2007) values reported are for peak flows and annual water yield change is likely lower, and that for Bethlahmy (1974, 1975) canopy cover reduction was up to 80% and average canopy cover reduction is likely much lower. Also shown is the relationship between canopy cover reduction by harvest and water yield increase (dashed line), calculated from the dataset of Stednick (1996).

have occurred when coniferous forest cover was removed in mesic environments, while removal of 'scrub' cover elicited the smallest response across a variety of climates (Brown *et al.*, 2005; see also hypotheses in Huxman *et al.*, 2005).

The seasonality of precipitation and streamflow in a watershed determined the season that experienced the greatest shifts in water yield after treatment (Brown *et al.*, 2005). For example, in watersheds where most precipitation occurred in summer, forest removal increases in annual water yield were driven by proportionally higher increases in summer water yield. Likewise, for watersheds dominated by snowmelt peak flows, tree harvest increased annual water yield through higher and earlier snowmelt peak flow (Brown *et al.*, 2005; Zou *et al.*, 2010).

Ecohydrological responses to die-off vary substantially and are much more inconsistent than well-reviewed responses to forest harvest (Figure 2). In particular, initial responses of decreased streamflow following canopy loss from die-off in drier forests are not seen in response to forest harvest, suggesting caution should be used in overgeneralizing from these results. Specifically, the finding of decreased streamflow following mortality in the piñon-juniper ecosystem (Guardiola-Claramonte, 2009; Guardiola-Claramonte *et al.*, in press) contrasts with previous tree removal research in watersheds of the same vegetation type. At the Beaver Creek experimental watershed in northern Arizona, two watershed treatments where 100% of tree cover was removed by harvest resulted in unchanged flows (Clary *et al.*, 1974; Baker, 1984). A third watershed was treated with an herbicide targeted at junipers that removed 83% of tree cover. This increased annual streamflow initially by 65% in 4 years post-treatment (Clary *et al.*, 1974) and by 157% over 8 years post-treatment (Baker, 1984). The larger watersheds considered in the recent die-off study also include some higher-elevation, mesic forests (Guardiola-Claramonte, 2009; Guardiola-Claramonte *et al.*, in press). Changes in precipitation dynamics at high elevations could have exerted a disproportionate influence on whole basin water yield numbers following piñon die-off (Guardiola-Claramonte, 2009; Guardiola-Claramonte *et al.*, in press). On the other hand, at Beaver Creek, in addition to killing junipers, the herbicide treatment also initially damaged piñon pines and led to a shift in the understorey from perennial to annual grasses (possibly further depressing T); harvested watersheds also were subjected to some burning of slash (Clary *et al.*, 1974; Baker, 1984). Other assessments of water yield response to tree removal in piñon-juniper watersheds found that ETI still accounted for almost all precipitation following treatment, and that flows did not increase unless slash was burned (Gifford, 1975; Wright *et al.*, 1976). Assessment of other shrub-dominated watersheds suggests that subsurface characteristics which permit deep drainage of soil water are key to determining if shrub removal leads to increased streamflow (Wilcox, 2002; Seyfried and Wilcox, 2006; Wilcox *et al.*, 2006).

In summary, studies of die-off effects on indirectly affected hydrological processes are limited in scope and not always consistent with relevant harvest study results, perhaps due to a variety of factors. Inconsistencies in measuring and reporting canopy cover loss among die-off studies may also be contributing to the variability in responses: it is easier to measure the impact of an externally applied forest harvest than to quantify a tree mortality event that varies greatly with space and time. We hypothesize that the interaction of three influences—annual precipitation, level of canopy loss, and belowground characteristics—determines many of the ecohydrological differences among studies of responses to tree cover loss both within and between die-off and harvest responses, all of which will vary with successional dynamics.

THE PERSISTENCE OF ECOHYDROLOGICAL EFFECTS FROM DIE-OFF

Persistence of die-off effects

The persistence of hydrological responses to tree mortality through time will depend on the trajectory of each

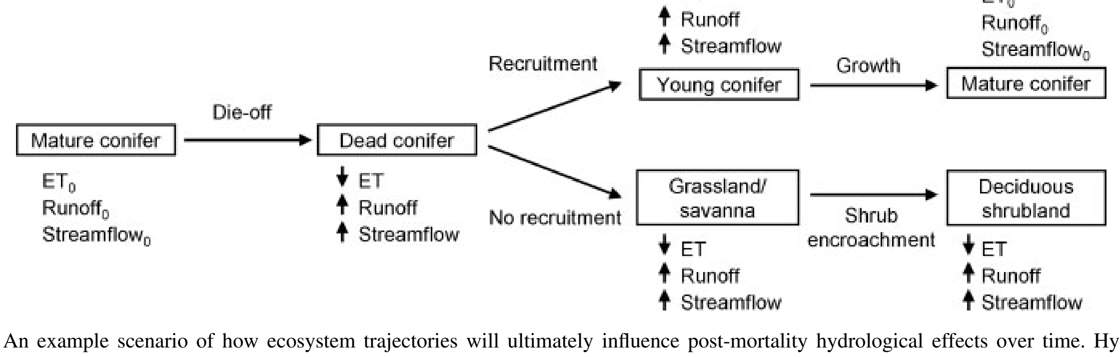

Figure 3. An example scenario of how ecosystem trajectories will ultimately influence post-mortality hydrological effects over time. Hydrological outcomes over longer time-scales depend on whether disturbance from die-off is sufficient to cross a threshold that triggers a shift to an alternate state of ecosystem structure and function (Ryan *et al.*, 2008). Arrows next to water budget components indicate relative change from the initial forest community. After mature conifer forest die-off episodes, the relative success of conifer recruitment can determine whether the forest returns to its previous composition, structure, and hydrological function or transforms into an alternative state such as an open savanna or a deciduous shrubland with lower ETI and higher runoff and streamflow than the initial forest state. Adapted for die-off and hydrological function from Goetz *et al.* (2007).

ecological response to die-off. Ecological responses following mortality of a high percentage of overstorey trees could range from a successional return to previous community structure and composition to an emergence of a new community with an altered ecosystem function (Figure 3). Predicting ecological responses to die-off in a changing climate is inherently difficult as multiple life-stage, survival thresholds are affected (Jackson *et al.*, 2009), as are cross-scale interactions with other ecological disturbance processes (Allen, 2007). One of the few, if not the only, study to date measuring the long-term effect of die-off on hydrological processes showed the persistence of a 10% increase in water yield in two Colorado watersheds for 25 years following a bark beetle outbreak that caused up to 80% tree mortality (Bethlahmy, 1974). Long-term ecological responses to tree die-off are poorly understood (Allen *et al.*, 2010), but will ultimately determine the persistence of any mortality-induced hydrological changes.

Observed vegetation responses following tree mortality vary and are mostly short-term. Sites in the southwest United States affected by piñon pine die-off underwent a resetting of a successional trajectory (Clifford *et al.*, 2011), show little immediate recruitment of overstorey trees (Barger *et al.*, 2009), and were chronically affected by episodic mortality (Mueller *et al.*, 2005) but exhibited a rapid understorey growth response (Rich *et al.*, 2008). At many sites affected by die-off in British Columbia, recruitment of ponderosa and lodgepole pine seedlings and saplings, many of which survived the die-off event, are expected to restore forest cover (Klenner and Arsenault, 2009; Axelson *et al.*, 2009, 2010; Brown *et al.*, 2010), although changing climate could preclude this (Loarie *et al.*, 2009). Shifts in dominance patterns of tree species are also possible if recruitment of a drought-tolerant species follows mortality that primarily affected a codominant, less drought-tolerant species (Suarez and Kitzberger, 2008). For such watersheds, the pace of tree recruitment will determine persistence of the initial hydrological effects of die-off.

Die-off may increase the vulnerability of an ecosystem to additional disturbances such as biological invasion or fire that would have further ecohydrological consequences (Mack *et al.*, 2000; Allen, 2007). Tree mortality could create the conditions for invasion of novel and alien species into watersheds though dynamic changes in the diversity–invasibility relationship (Clark and Johnston, 2011). Invasive species, whether woody or herbaceous, could further affect post-mortality watersheds by altering hydrological processes in unexpected ways (Wilcox and Thurow, 2006; Boxell and Drohan, 2009; Wilcox, 2010). Tree die-off also affects fire dynamics in multiple ways—e.g., initially decreasing crown fire risk as dead canopies drop flammable fine fuels, but conversely increasing surface fire risk as this organic litter reaches the forest floor and understorey vegetation increases (Allen, 2007; Bentz 2009). High-density tree recruitment following overstorey mortality could create conditions that increase crown fire risk. Fire following mortality would further alter other water budget component responses (Shakesby and Doerr, 2006), potentially with greater consequences than die-off (See Table I, and its earlier discussion.)

Other relevant research on persistence of effects. In paired catchment studies that include forest manipulation, the persistence of increases in water yield attributed to the loss of overstorey T depended on both management after treatment (Brown *et al.*, 2005) and climate (Troendle *et al.*, 2010). In colder climates, where regeneration is slower, streamflow effects may last many decades (Troendle and King, 1987). When regeneration of forest cover occurs rapidly, initial increases in streamflow typically persist for less than a decade, and in some cases water yield may eventually decrease below pre-treatment levels, particularly following species conversion treatments (Hornbeck *et al.*, 1993; Jones and Post, 2004; Brown *et al.*, 2005). Conversely, for some watersheds where forest clearing resulted in negligible or small initial changes in water yield, water yield increased for 10–20 years following regrowth or afforestation, possibly due to reduced T, before appearing to reach a new equilibrium (Brown *et al.*, 2005).

MANAGEMENT IMPLICATIONS AND OPTIONS

Options for land managers dealing with hydrological changes following die-off will likely differ with climate and forest type, and will need to be considered in the context of site-specific objectives. For some regions, increased water yield caused by tree die-off could be desirable, as long as water quality is unaffected and peak flows do not cause excessive flooding. In other regions, preventing die-off from causing decreased water yield, water quality reduction, or flooding damage may be the goal. However, the current state of knowledge on the hydrological impacts of die-off precludes precise prediction of the effects on a specific watershed.

Preventing broad-scale forest die-off through forest management may not be feasible due to the great extent of potentially affected areas, which makes management actions cost-prohibitive and logistically difficult. For example, spraying trees with pesticides to reduce bark beetle success can be very effective, yet is probably limited only to high value areas due to expense and risks of negative environmental side-effects (Fettig *et al.*, 2006). Forest thinning has long been suggested as a management strategy for reducing vulnerability of trees to drought and pests (see Fettig *et al.*, 2007; Millar *et al.*, 2007). Thinning can result in increased soil moisture per tree (or per leaf area or unit biomass), as seen in ponderosa pine forests (Feeney *et al.*, 1998; Simonin *et al.*, 2007; Zou *et al.*, 2008). However, research findings on the effect of stand density on mortality rates are mixed. A number of studies have shown that mortality increased with tree density (Fettig *et al.*, 2007; Greenwood and

Weisberg, 2008; Horner *et al.*, 2009; Klos *et al.*, 2009; Negron *et al.*, 2009), yet others have found no relationship between density and mortality (Mueller *et al.*, 2005; Floyd *et al.*, 2009). Therefore, the effectiveness of thinning for preventing tree die-off may depend on the density-dependence of mortality drivers, species traits, and the type of thinning used (Waring and Pitman 1985; Fettig *et al.*, 2007; Allen *et al.*, 2010). For example, a thinning from below to remove small trees can reduce competition for soil water and drought stress on large trees (McDowell *et al.*, 2006). Such a treatment would be most effective in forests where drought is the dominant cause of tree mortality and less effective where pests and/or pathogens cause mortality independent of tree drought stress. Thinning to prevent undesirable die-off-induced hydrological changes could be self-defeating, if effective treatment requires high levels of tree removal that would cause hydrological changes on their own. Many areas vulnerable to die-off may also be at risk of high severity fire from a legacy of fire suppression, and thinning can be an effective method to reduce the risk of fire impacts (Covington *et al.*, 1997), which include hydrological changes that exceed those of die-off (See earlier discussion).

Post-mortality options for mitigating undesirable hydrological effects will likely consist mostly of trying to guide the ecological trajectories of watersheds following die-off (Millar *et al.*, 2007). Restoring a watershed's water balance to pre-die-off conditions potentially could be achieved by encouraging recruitment and regrowth that leads to recovery of forest cover that existed prior to mortality. However, ongoing climate changes may mean that a different mix of future tree species should be considered to enhance probabilities of future forest sustainability. For large undesirable hydrological impacts such as flooding, planting of non-native fast-growing tree species may present a short-term local solution at local spatial scales, but the expense of treating large areas and the time lag between tree planting and mitigating eco-hydrological effect both limit the potential of such an approach. Additionally, the risks of undesired long-term hydrological and ecological effects from such an action, which could include altered flows and habitat loss, can be high. In regions with extensive die-off, lack of resources

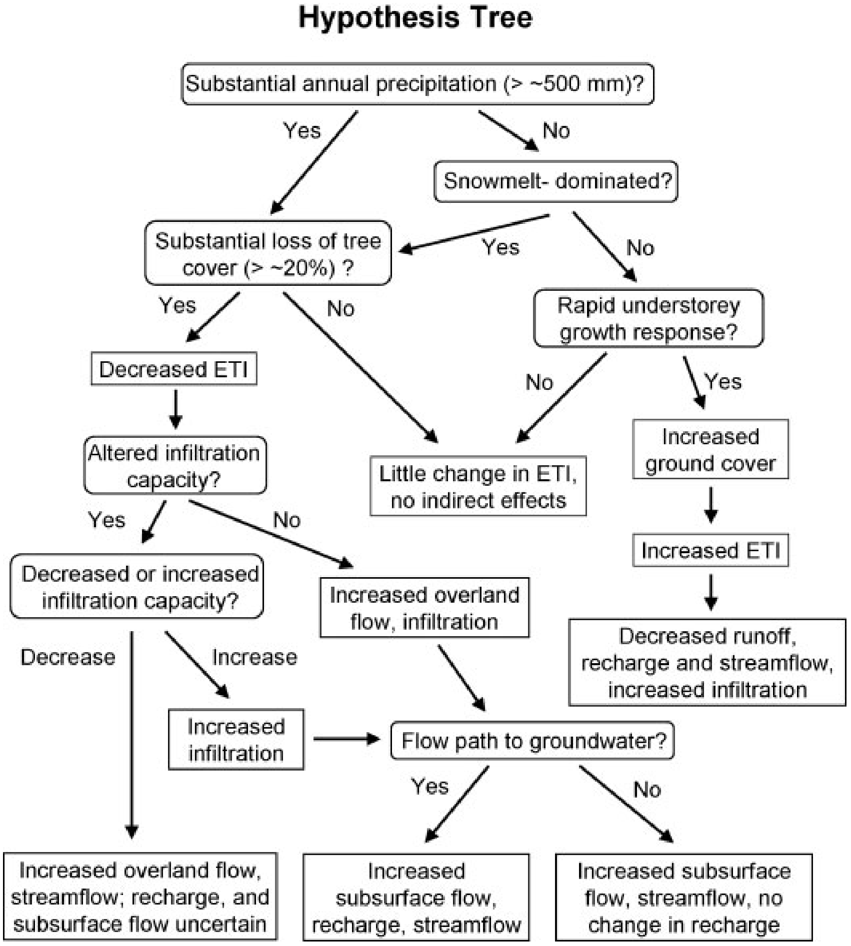

Figure 4. A hypothesis tree of potential effects of tree die-off on key water budget components. Possible effects include increases and decreases in ETI, runoff, infiltration, groundwater recharge, subsurface flow, and streamflow following tree mortality. Important factors for determining these outcomes include an annual precipitation threshold at 500 mm, the dominance of snowmelt on watershed flows, percent tree cover lost from mortality, understorey growth and transpiration response, the effect of tree mortality on infiltration capacity, and the existence of subsurface groundwater flow paths. Testing these hypotheses will require modelling assessments and empirical studies in watersheds affected by die-off that vary widely in climate, forest type, and soil properties.

will limit mitigation of these risks, necessitating adaptation to post-mortality hydrological conditions.

When die-off occurs in forests of commercially valuable timber, salvage logging is often considered a means of recovering financial losses. In the extensive post-mortality forests of British Columbia, salvage harvesting of lodgepole pine is now proceeding at a massive scale (Carver *et al.*, 2009a,b). This harvesting includes removal of standing dead trees as well as the cutting of live, higher value, unaffected tree species. Salvage logging could amplify hydrological changes brought on by tree mortality, initially through road-building and associated soil compaction and disturbance, as well as through additional live tree removal, and over the long term by affecting forest ecological trajectories that otherwise would lead to restoration of hydrological function. Modelling assessment of the Fraser River Basin in British Columbia suggests that salvage harvesting could double post-mortality increases in peak flows (Carver *et al.*, 2009a; Weiler *et al.*, 2009). Therefore, forest managers should consider the potential for undesirable hydrological impacts when planning post-mortality salvage harvest. More generally, the limited management options for preventing tree die-off across extensive areas highlight the importance of future research to improve our ability to predict the ecohydrological consequences of die-off.

EMERGENT HYPOTHESES AND RESEARCH NEEDS

Our evaluation of the small group of published studies on hydrological responses to die-off, considered in concert with the larger body of research on forest harvest effects, reveals a wide range of possible outcomes. With the aim of guiding and prioritizing future research, we present a set of simplified hypotheses that are generally consistent with the existing die-off studies, applying insights from the other relevant research reviewed. We present these as a hypotheses tree (Figure 4). Note that these are hypotheses for future testing rather than validated conclusions. The research summarized above suggests that the most likely direct effect of tree mortality is a reduction in ETI and an associated indirect increase in flows and groundwater recharge (Stednick, 1996; Zhang *et al.*, 2001; Brown *et al.*, 2005; see also Table II). Notably, however, in drier regions, which includes many areas where mortality is occurring (Allen *et al.*, 2010), die-off may not cause significant increases in water yield (Guardiola-Claramonte, 2009; Somor, 2010; Guardiola-Claramonte *et al.*, in press; consistent with Zhang *et al.*, 2001; Wilcox, 2002; Wilcox *et al.*, 2006). Therefore, we hypothesize that watersheds receiving more than ~500 mm of annual precipitation will experience decreases in ETI from a loss of overstorey T and I that lead to increased annual flows and potential groundwater recharge, while watersheds with less than ~500 mm of annual precipitation will not (Figure 4, consistent with Zhang *et al.*, 2001). However, for watersheds with less than ~500 mm of precipitation that also have water yields dominated by snowmelt, we hypothesize that die-off will produce increased flows (Figure 4, Carver *et al.*, 2009a; Weiler *et al.*, 2009).

The hydrological consequences of tree mortality also will likely depend on the level of canopy cover reduction. Harvest-related literature suggests a threshold of ~20% loss of forest cover is required to statistically detect a change in water budget components (Stednick, 1996; Brown *et al.*, 2005). We hypothesize that this threshold of ~20% loss of forest cover for producing a detectable change in water budget components also applies to die-off (Figure 2). Mortality in many die-off affected areas falls below this threshold (Allen *et al.*, 2010), and we hypothesize such watersheds will not experience much hydrological change. We also hypothesize that seasonal effects on watershed responses following die-off will be similar to those reported in response to harvest (Brown *et al.*, 2005), with annual changes in water yield depending on peak flows (Figure 5), particularly where snowmelt dominates watershed dynamics. This hypothesis is consistent with a modelling assessment of bark beetle effects in the Frasier Basin, British Columbia, Canada (Carver *et al.*, 2009a,b). Exceptions to this seasonal effect might exist when mortality selectively kills species with a unique hydrological function, as highlighted in the case of die-off of eastern hemlock in the southeast United States (Ford and Vose, 2007). Because eastern hemlock is the only evergreen species in an otherwise deciduous forest, its loss is hypothesized to reduce early spring T, causing increased spring flows that could raise annual water yield (Figure 5).

In addition, we hypothesize that the causes of tree mortality can influence potential ecohydrological outcomes. When drought is an important cause of tree mortality, we expect reduced precipitation from drought to mute ecohydrological responses (Guardiola-Claramonte, 2009; Somor, 2010; Guardiola-Claramonte *et al.*, in press;). In

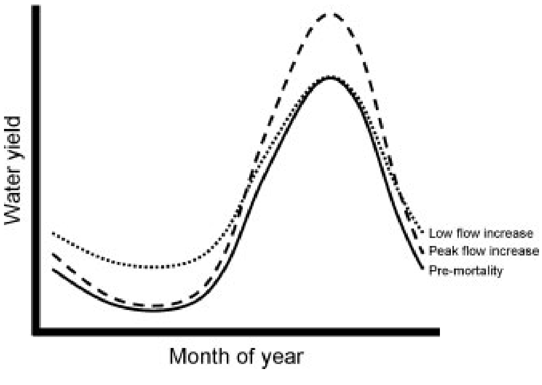

Figure 5. A depiction of two possible seasonal affects on annual water yield following die-off. Post-mortality, annual water yield increases from pre-mortality flows (solid line) could be caused primarily by increased peak-flows (dashed line) or by increased low flows (dotted line). Peak flow increases are more likely following die-off, especially for watersheds where flows are dominated by snowpack dynamics (Brown *et al.*, 2005; Carver *et al.*, 2009a,b). Loss of species that play a unique hydrological role in the seasonality of watershed flows could alter seasonal patterns of ETI, and by extension water yield, affecting annual totals through increased low flows (Ford and Vose 2007).

Table III. Research priorities to address key uncertainties that currently limit development and testing of hypotheses regarding the ecohydrological consequences of tree die-off.

Research priority	Description
Follow-up catchment studies	More catchment studies of mortality-affected watersheds using existing gauge data are needed for a wide variety of climates, forest types, and affected species. The extent of recent die-off makes it probable that such results already exist from currently monitored watersheds, or could be obtained from re-starting measurements at previously instrumented watersheds.
Persistence of effects over ecological trajectories	Hydrological and ecological monitoring post-mortality are needed to determine the persistence of die-off hydrological effects and their dependence on ecological changes. Such studies should also examine how ecological changes following mortality depend on post-mortality hydrological changes so that ecohydrological feedbacks can be considered.
ETI partitioning	Research partitioning the stand-level effects of ETI into its E, T, and I components following tree die-off could be done through experimentally killing trees within an intensely instrumented eddy covariance tower footprint to compare ETI components before, initially after treatment, and following post-mortality ecological responses.
Flowpath partitioning of indirectly affected components	Investigation should also focus on flowpath partitioning of the lesser-studied indirect effects of tree mortality such as saturation excess and Hortonian overland flow, subsurface flow, and groundwater recharge, and groundwater flow following tree die-off.
Modelling large ungauged areas to scale hydrological effects	More modelling assessments are needed that incorporate existing and new empirical data to scale hydrological effects across large areas. Such models should be coupled with atmospheric models to better understand the comprehensive water budget and runoff dynamic effects of tree die-off at sub-continental scales.

contrast, when mortality occurs without a change in precipitation but is primarily driven by pest or pathogen outbreak, we expect ecohydrological effects will be more similar to harvest responses. Given that tree die-off could ultimately affect a very large proportion of the world's forested area (Allen *et al*., 2010; Gonzalez *et al*., 2010), we expect there will be substantial cumulative hydrological effects. Consequently, building on the hypothesis tree presented, we suggest research priorities in four key areas (Table III). These include specific aspects related to follow-up catchment studies in watersheds that have experienced recent mortality; evaluation of the persistence of such effects over subsequent ecological trajectories; flow path partitioning investigations, including ETI partitioning; and improved modelling of large ungauged areas (all detailed in Table III).

In conclusion, episodes of regional-scale tree die-off around the world have been recently documented and likely provide a glimpse into the range of potential hydrological responses that may accompany die-off. Increased die-off is projected to occur with climate change, necessitating a rapid improvement in our ability to understand and predict how tree die-off affects watersheds. In particular, although we know tree mortality directly affects the E and T components of ETI though canopy cover loss and can alter the snow accumulation and melt dynamics of a watershed, how the net direct effects of die-off will be translated through changes in the water balance to indirect effects on soil moisture status, groundwater recharge dynamics, and streamflow volume and timing are unclear and require future research. The direct and indirect hydrological consequences of tree die-off in combination with temperature and precipitation shifts may exceed the hydrological effects of climate change alone, and for some regions could present risks to water resources. Post-mortality successional dynamics will ultimately determine if short-term die-off impacts to hydrological function will persist, be diminished, or altered further over longer time scales. Although management options for preventing die-off may be limited, development of policies to mitigate potential effects and restore watershed function will depend on a better understanding of the hydrological consequences of tree die-off. The hypotheses and research priorities we present provide a roadmap to help address this emerging core challenge in ecohydrology.

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