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# Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes

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Recent, large-scale outbreaks of bark beetle infestations have affected millions of hectares of forest in western North America, covering an area similar in size to that impacted by fire. Bark beetles kill host trees in affected areas, thereby altering water supply, carbon storage, and nutrient cycling in forests; for example, the timing and amount of snow melt may be substantially modified following bark beetle infestation, which impacts water resources for many western US states. The quality of water from infested forests may also be diminished as a result of increased nutrient export. Understanding the impacts of bark beetle outbreaks on forest ecosystems is therefore important for resource management. Here, we develop a conceptual framework of the impacts on coupled biogeophysical and biogeochemical processes following a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in lodgepole pine (*Pinus contorta* Douglas var *latifolia*) forests in the weeks to decades after an infestation, and highlight future research needs and management implications of this widespread disturbance event.

Current bark beetle outbreaks in western North American forests have reached levels not reported in the past, with affected areas in western US states covering in excess of 4 million hectares (USDA Forest Service 2010) and 14 million hectares in the western Canadian provinces (Safranyik *et al.* 2010), an area approximately equal to that

## In a nutshell:

- Bark beetle disturbances differ from fire or logging disturbances because bark beetles alter forest functioning without immediately affecting forest leaf area or stem density
- Understanding the cascading ecosystem impacts of bark beetle outbreaks requires knowledge of the impacts on coupled biogeophysical and biogeochemical processes
- Critical biogeophysical impacts include changes in water and energy cycling, and alterations to the ecosystem services associated with water supply
- Critical biogeochemical impacts include changes in carbon and nitrogen cycling, and alterations to the ecosystem services associated with carbon sequestration

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of Washington State (Figure 1). Although these bark beetle species are native to the coniferous forests of western North America, epidemics have been facilitated by recent climate change, including increased winter minimum and year-round temperatures and droughts (Breshears *et al.* 2005; Bentz *et al.* 2010); as a result, outbreaks of some species have moved to higher elevations (Logan *et al.* 2010) and higher latitudes (Safranyik *et al.* 2010). The annual area affected by bark beetle infestations in North America is comparable to the average area burned by fire (Kurz *et al.* 2008; USDA Forest Service 2010; Stinson *et al.* 2011), suggesting that the impacts of these outbreaks on biogeophysical and biogeochemical processes are of a similar magnitude to that of fire.

Bark beetle attacks impact energy, water, carbon (C), and nitrogen (N) cycling without immediately altering the physical structure of forests, thus differing from fire or logging disturbances (Brown *et al.* 2010; Pugh and Small 2012); insect outbreaks may last 3–5 years or more, whereas fire and logging events occur over much shorter time periods, after which the stand leaf area and stem density are substantially reduced through the combustion of biomass or removal of stems from the site. Insect outbreaks affect both biogeophysical and biogeochemical processes (Mitchell and Priesler 1998; Kurz *et al.* 2008; Brown *et al.* 2010; Pfeifer *et al.* 2011; O'Halloran *et al.* 2012; Pugh and Small 2012). Critical biogeophysical impacts include changes in water and energy cycling, such as the partitioning of precipitation into interception, runoff, soil storage, and recharge, and modifications to processes related to energy (surface albedo) and water fluxes (evaporation, transpiration, and sublimation). In addition, canopy drag (wind speed reduction caused by vegetation roughness) on the atmosphere is altered as the coniferous trees lose needles and as the dead standing trees fall.

Likewise, critical biogeochemical impacts include reductions in plant C uptake, increases in decomposition, and potential loss of nutrients. An example of "coupled" biogeophysical and biogeochemical processes is the influence of canopy structure (leaf area and stem density) on the amount of precipitation captured by the foliage (and therefore on soil moisture), the effects of soil moisture on soil decomposition and plant growth, and the interaction between soil nutrients, decomposition, and plant growth (Figure 2).

Biogeophysical and biogeochemical impacts following bark beetle infestation have the potential to severely affect both natural resources and economic values. For example, snow from mountain ecosystems is the major source of water for more than 60 million people in the western US and Canada (Bales *et al.* 2006); changes in forest structure following bark beetle epidemics alter the amount, timing, and partitioning of this resource (Rex and Dubé 2006; Pugh and Small 2012). Post-insect-infestation tree mortality also affects C and N cycling in forests. Although most of these forests are net C sinks (eg Schimel *et al.* 2002), insect-related disturbances may cause them to release C to the atmosphere (Kurz *et al.* 2008). Nutrient cycling within affected forest ecosystems will also be modified, with reduced plant uptake increasing water and nutrient export. As a result, the aggregate impact of insect outbreaks may have consequences for regional and global weather and climate systems as well as for water supply and C storage.

Here, we present a chronological model of ecosystem impacts to help inform future management decisions and to identify future research areas that will improve understanding of insect-related disturbances. Our model focuses on the characteristic time scales of a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in lodgepole pine (*Pinus contorta* Douglas var *latifolia*) forests (Figure 2), beginning in the initial days and weeks after infestation (Stage 1; Figure 3a), proceeding through a phase in which needles turn red in the months to years following the outbreak (Stage 2; Figure 3b), to the gray phase that occurs as needles fall off dead trees within 3–5 years following attack (Stage 3; Figure 3c), and finally to tree regeneration and snagfall in the decades following the outbreak (Stage 4; Figure 3d). Pine stands that are affected by mountain pine beetle infestations are typically dominated by lodgepole pines (>80% of the stem density), although spruce (*Picea* spp) and fir (*Abies* spp) are also found therein. Understory vegetation may be extensive in some stands (eg Brown *et al.* 2010). We anticipate that our conceptual model will provide a framework for future investigations of the impacts of bark beetles on forest ecosystems.

## ■ Coupled biogeophysical and biogeochemical impacts

### Stage 1: green attack (days to weeks)

Mountain pine beetles preferentially infest and kill larger diameter host trees (pines), leaving smaller diameter trees
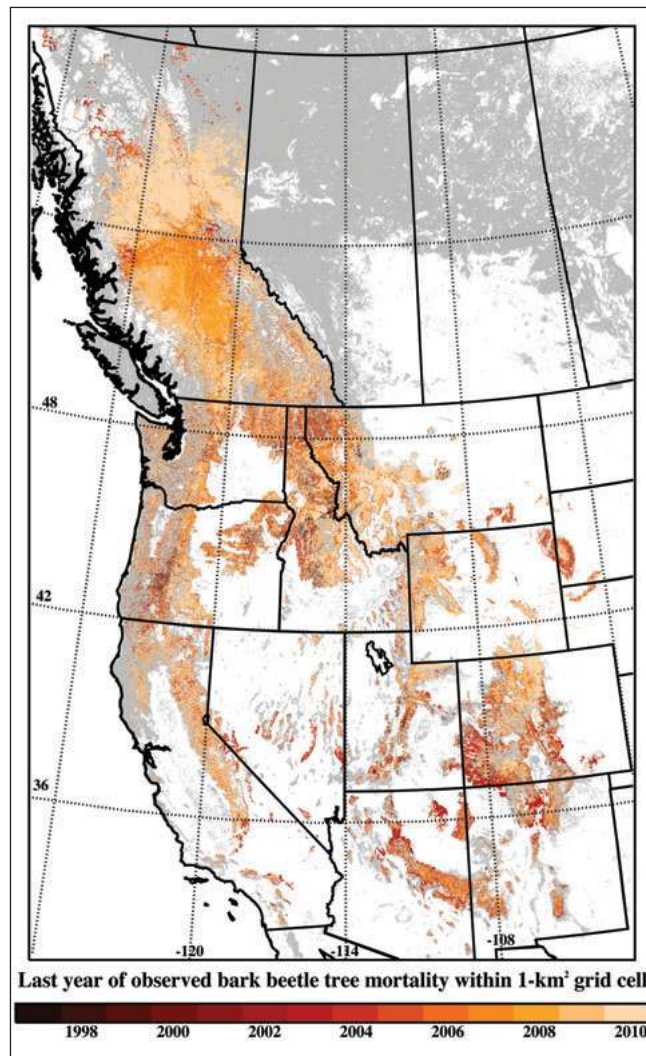


**Figure 1.** *Areas affected by bark beetles from 1997–2010 (in the western US) and 2001–2010 (in British Columbia, Canada). Color of each grid cell represents the last year that bark beetle damage was observed by aerial surveys.*

and understory vegetation unaffected (Shore and Safranyik 1992). Beetles introduce blue stain fungi (*Grosmannia clavigera*) into tree xylem, which decrease and eventually prevent water transport (Paine *et al.* 1997). Sap flux studies have shown that a drop in transpiration occurs within one month of infestation and that the rate of change is dependent on fungal virulence (Yamaoka *et al.* 1990). This finding contrasts with experimentally girdled trees (simulating beetles feeding on phloem) that took up to five growing seasons to die, whereas those inoculated with blue stain fungi died in one growing season (Knight *et al.* 1991).

The initial impact of mountain pine beetle-induced mortality on lodgepole pine trees is hypothesized to occur in three stages. First, water transport in the stem shuts down, which results in the same response of stomatal closure as tree response to drought. Stomatal conductance and plant hydraulics are closely coordinated (Ewers *et al.* 2007). Second, a drop in stomatal conductance leads to a
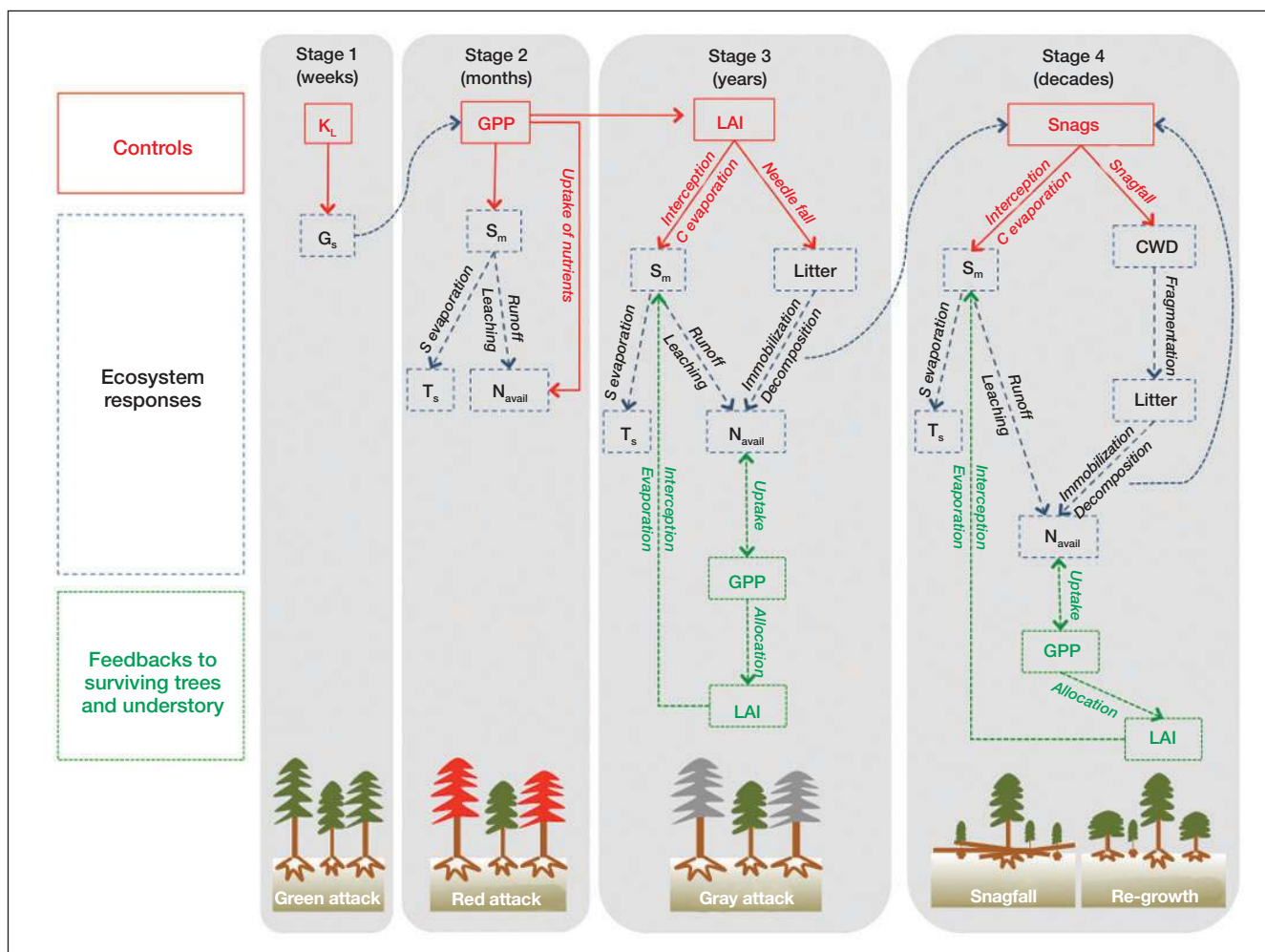
***Figure 2.*** *Impacts of mountain pine beetle outbreaks on coupled water, C, and N cycles in lodgepole pine ecosystems. Red solid lines indicate controls at each stage, blue dashed lines indicate ecosystem responses, and green dotted lines indicate the feedbacks to surviving trees and understory. $K_L$ = tree hydraulic conductance; $G_s$ = stomatal conductance; $S_m$ = soil moisture; $T_s$ = soil temperature; $N_{avail}$ = available nutrients; LAI = leaf area index; GPP = gross primary productivity; CWD = coarse woody debris; S evaporation = surface evaporation; C evaporation = canopy evaporation.*

drop in photosynthesis because of $CO_2$ limitation (Flexas *et al.* 2004). Third, attacked trees die of C starvation due to lack of $CO_2$ as a result of reduced stomatal conductance (Adams *et al.* 2009; McDowell 2011), hydraulic failure (Sala and Hotch 2009; Sala *et al.* 2010), or a combination of the two (McDowell *et al.* 2011). Additional research is needed to determine the specific mortality mechanism (McDowell *et al.* 2011).

The decrease in water uptake described above leads to several mountain pine beetle/blue stain fungus impacts on lodgepole pine during the epidemic's tree mortality phase. Lower hydraulic conductance within affected trees causes a reduction in N uptake, and reduced N availability further decreases hydraulic conductance, causing a feedback loop (Ewers *et al.* 2000). Tree hydraulic conductance prompts reductions in stomatal conductance during the weeks immediately after successful bark beetle colonization of a stand (Figures 2 and 4). In severe outbreaks, the reduced stomatal conductance of affected trees cascades from the tree to the canopy to the ecosystem.

## Stage 2: fading trees and red attack (months)

During this stage, stand structure (leaf area and stem density) remain unmodified (Figure 5); however, cascading ecosystem impacts begin. As stomatal conductance declines in infested trees and as more trees are killed within a stand, the magnitude of impacts expands to the ecosystem scale (Figure 2). We hypothesize that evapotranspiration rates measured by eddy covariance will decline approximately in proportion to the amount of mortality that occurs within the footprint of the eddy-covariance tower during the months following the outbreak, initially driven by a decline in transpiration (Figure 4). The degree to which tree-scale impacts will cascade to ecosystem-scale processes will depend on the number of trees killed, understory characteristics, and pre- and post-disturbance stand structure.

We also hypothesize that the rapid decline in tree transpiration will leave more water in the soil within the first few months post-outbreak (Figure 4; Clow *et al.* 2011).
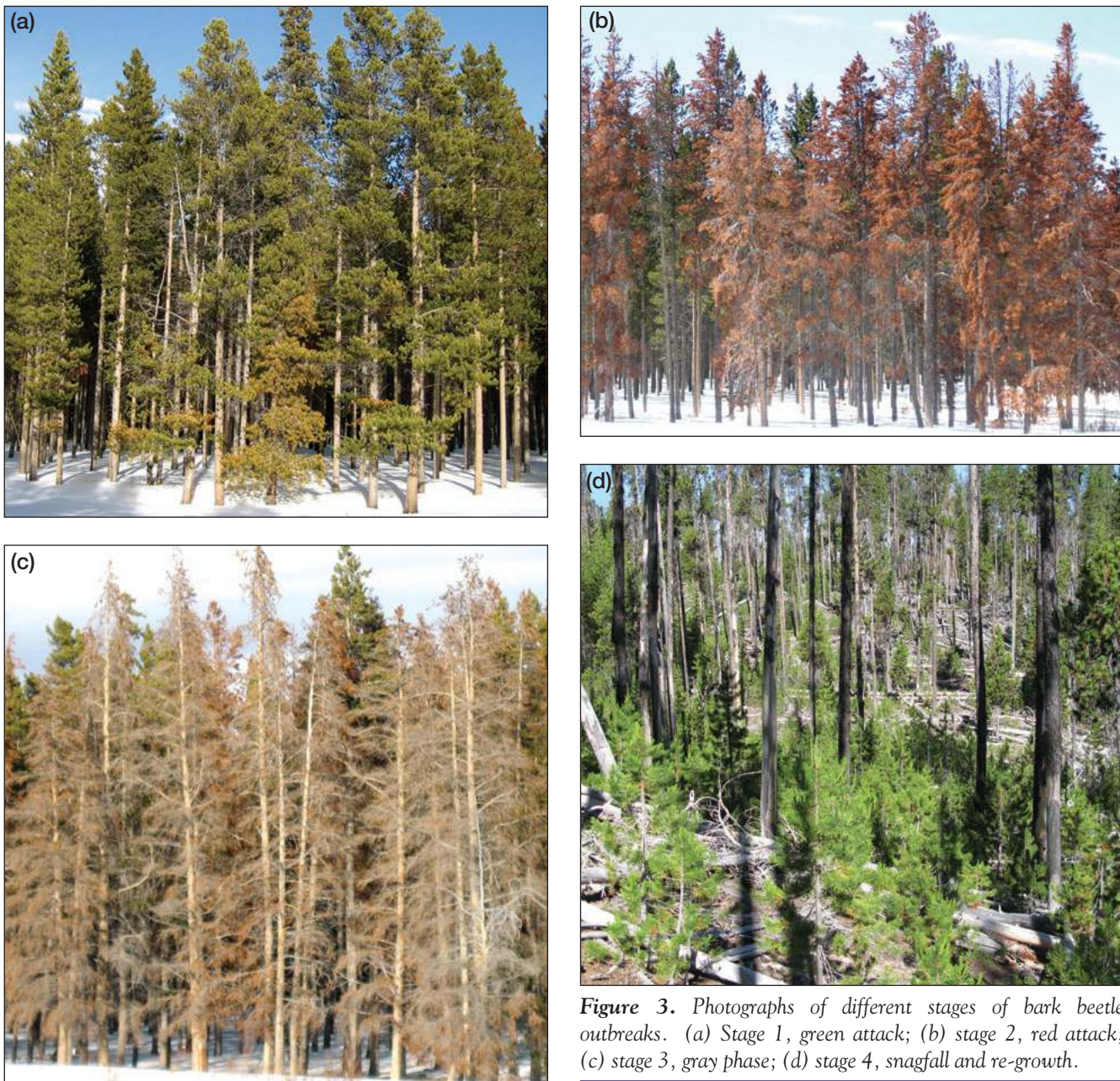
**Figure 3.** *Photographs of different stages of bark beetle outbreaks. (a) Stage 1, green attack; (b) stage 2, red attack; (c) stage 3, gray phase; (d) stage 4, snagfall and re-growth.*

Lodgepole pine forests are typically water-limited during the middle and late growing season (Knight *et al.* 1985; Fahey and Knight 1986), but in the first summer of attack we anticipate soil moisture to remain elevated (Morehouse *et al.* 2008). Growing-season soil moisture is hypothesized to be highest during Stage 2 as transpiration is reduced, while the now-red canopy shades the ground and minimizes atmospheric turbulence at ground level in the same fashion as an uninfested stand, reducing soil evaporation. Higher soil water contents are expected to reduce soil and litter temperatures and moderate the daily and seasonal variations of soil and litter moisture (Griffin *et al.* 2011). We believe that the increased soil moisture content and lower temperatures play key roles in the coupling between biogeophysical and biogeochemical processes (eg plant growth and decomposition; see coupling in Figure 2),

which initiates ecosystem-scale impacts.

Altered soil moisture and temperature, together with reduced uptake of nutrients by trees, initial root death, and inputs of relatively N-rich litter, are expected to increase the amounts of mineral N available in soils within just a few months of the outbreak (Figure 6; Clow *et al.* 2011; Griffin *et al.* 2011). Extractable nitrate and ammonium concentrations will increase until microbial immobilization and plant uptake rates increase. These elevated concentrations will likely reduce plant hydraulic conductance as a result of lower root-to-leaf area ratios and higher resistance to cavitation (Ewers *et al.* 2000), both of which will limit how rapidly plant transpiration increases with succession. High resin-ammonium accumulation and/or soil nitrate concentrations have been reported by Morehouse *et al.* (2008), Clow *et al.* (2011),
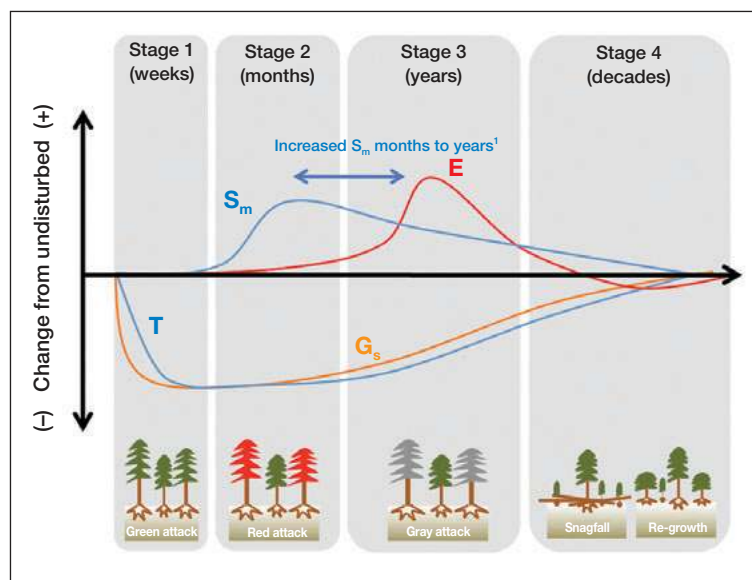
**Figure 4.** *Time series of changes to stomatal conductance ($G_s$), transpiration (T), evaporation (E), and soil moisture ($S_m$) during and following mountain pine beetle-caused mortality in a lodgepole pine forest. [1]Morehouse* et al. *(2008) reported increased soil moisture after a bark beetle outbreak in a ponderosa pine (Pinus ponderosa) forest in the months to years following attack.*

and Griffin *et al.* (2011). This initial response has been observed in many forested ecosystems following disturbance (eg Likens *et al.* 1978) and demonstrates a potential for loss of nutrients from the system in either gaseous or dissolved form.

Forest–atmosphere C exchange will continue to change in the months following beetle-caused tree mortality. Plant C uptake will fall; the magnitude of this change will depend on stand and outbreak characteristics, similar to stand-level evapotranspiration rates. Although modeling studies report large net C losses (Kurz *et al.* 2008), eddy covariance measurements indicate that surviving vegetation can maintain net C uptake for several years following beetle-induced mortality (Brown *et al.* 2010). Root respiration will decrease within months following an infestation, as belowground C allocation is initially low during and after disturbance (Goulden *et al.* 2011). Model simulations suggest the reduction of root respiration will lower total soil respiration (root plus decomposition) for months to years following the initial infestation, despite enhanced decomposition of fine roots as a result of the increased soil moisture content and high N availability (Edburg *et al.* 2011). However, Morehouse *et al.* (2008) measured a constant soil respiration within the first several months following attack, suggesting that the decreases in root respiration were compensated for by increases in decomposition fluxes.

### Stage 3: gray attack (years)

Dead trees typically enter the gray phase within 3–5 years of the initial infestation, as needles fall from killed trees (Amman *et al.* 1990). Needlefall causes a decrease in total leaf area (Figure 5), which has cascading impacts on cou-

pled biogeophysical and biogeochemical processes (Figure 2). That is, a drop in leaf area reduces the aerodynamic drag of the canopy, thereby reducing the amount of momentum (ie momentum of air) absorbed by the canopy and altering surface exchange fluxes (Edburg *et al.* 2010). A reduction in leaf area also decreases the amount of solar radiation (Musselman *et al.* 2008) and precipitation (Zhang *et al.* 2004; Pugh and Small 2012) caught by the foliage, resulting in increased sunlight and water available at the soil surface. We argue that these changes will lead to decreased sublimation of snow from the canopy and increased surface sublimation and evaporation as more radiation and momentum of air penetrate to the snow surface and ground surface (Musselman *et al.* 2008; Royer *et al.* 2011). Furthermore, snow redistribution will be substantially modified because it is a function of wind and turbulence within and above the forest (Stottlemyer and Troendle 1999). Peak soil moisture should occur earlier in the spring as the timing of snow melt changes (Molotch *et al.* 2009), whereas lower transpiration will allow soil moisture to remain elevated later into the growing season (starting in Stage 1; Figures 2 and 4). Surface soil moisture may become considerably more spatially variable as the increasingly patchy canopy results in locally enhanced solar input and turbulence, which, in turn, amplifies evaporation from the land surface. These increases will also partially offset reductions in transpiration (Gustafson *et al.* 2010; Royer *et al.* 2011).

Carbon and N cycling during the gray attack period is altered as a result of increased needle decomposition and continued root decomposition from Stage 2 (Edburg *et al.* 2011). Because decomposition and microbial uptake of N are dependent on soil temperature and moisture, the C and N cycles are strongly dependent on the aforementioned biogeophysical changes to canopy structure and water cycling during this stage (as shown in Figure 2). We further hypothesize that increased substrate availability from needle and root inputs to soil, which are greater than background rates (Edburg *et al.* 2011), will lead to increased decomposition (Figure 6). However, total soil respiration rates will continue to be suppressed unless decomposition rates increase enough to compensate for the loss of root respiration during this stage.

Given the potential compensating effects of changes in root respiration and decomposition, the response of surviving trees and understory vegetation is critical in determining the net ecosystem C balance during this stage (Romme *et al.* 1986; Brown *et al.* 2010; Pfeifer *et al.* 2011). As decomposition increases, N immobilized in microbial biomass may be retained in the ecosystem and potentially transferred to vegetation as microbial biomass turns over (Brooks *et al.* 1998). Alternatively, both denitrification (Brooks *et al.* 1997) and hydrologic N export (Brooks and

Williams 1999) may reduce plant-available N and limit the growth of regenerating vegetation. Increases in soil moisture, nutrients, and sunlight available to the understory are hypothesized to promote plant growth (Romme *et al.* 1986; Brown *et al.* 2010; Pfeifer *et al.* 2011; Royer *et al.* 2011). Because lodgepole pines can be limited by both water and N (Fahey and Knight 1986), we expect the net effect on productivity of increased water and sunlight and the variations in N availability to be site dependent because of differences in soil properties (water-holding capacity) and pre- and post-outbreak species composition (eg rates of transpiration; Fahey and Knight 1986). In some locations, surviving trees and understory vegetation respond favorably to increased water and N in the gray stage, whereas in other N-limited locations, further N losses may outweigh increases in sunlight or water and favor symbiotic N fixation by the understory, potentially postponing forest regeneration.

### Stage 4: snagfall and re-growth (decades)

Snags begin to fall and the understory and surviving trees increase growth rates (productivity) in Stage 4, as the decrease in canopy cover that began in Stage 3 continues (Figures 2 and 5). The rate of snagfall is a function of soil type, soil temperature and moisture, and tree species (Lewis and Hartley 2005). Canopy openings created by snagfall during this period accumulate more snow than surrounding forests because less snow is intercepted (caught) by the canopy (Golding and Swanson 1978) and wind re-deposition of snow increases (Stottlemeyer and Troendle 1999). As new seedlings and surviving trees grow during the following decades, the opening is filled in and interception of snow increases until the canopy is closed (Figure 5).

Additions of C from snags and coarse woody debris combined with labile C in fresh litter and root exudates will stimulate decomposition and thus immobilization of N (Figure 2; Harmon *et al.* 1986; Edburg *et al.* 2011). We expect the magnitude of the increases in decomposition and immobilization to be smaller than the increases in Stage 3 but they will be longer lasting because C and N from the snags will enter the soil at a slower rate and because the substrate quality is lower than that of roots and needles (Figure 6). Large C inputs to the soil from snagfall and high rates of N immobilization may lead to large belowground stores of C and N, which could be susceptible to groundwater N export as in Stage 3.

The availability of sunlight, water, and N will play a key role in the growth of understory vegetation, surviving trees, and tree seedlings (Fahey and Knight 1986; Romme *et al.* 1986). The rate of plant growth in this phase is also linked to snagfall (Figure 2). After snagfall, we expect increased sunlight to reach the surface and elevated soil
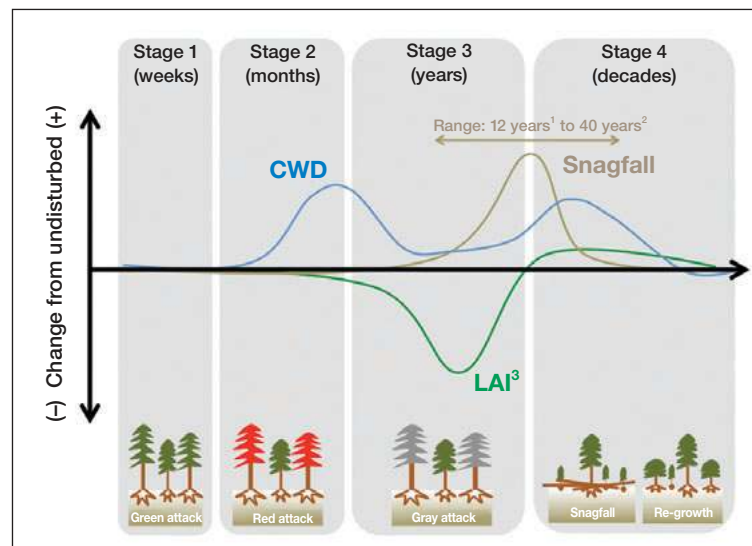


***Figure 5.*** *Time series of canopy structure changes (snagfall, leaf area index [LAI], and coarse woody debris [CWD]) after mountain pine beetle-caused mortality in a lodgepole pine forest. [1]Mitchell and Priesler (1998) – lodgepole pine in Oregon; [2]Angers et al. (2010) – jack pine (Pinus banksiana) in the boreal forest. [3]Mission et al. (2005) – ponderosa pine thinning experiment in California. Note: the first increase in CWD is from dead roots and the second is the result of an increase from snags.*

moisture, leading to enhanced plant growth over the decades in Stage 4. However, we also expect available N to play an important role in plant growth during this phase. Additional C inputs to the soil from snags will decrease C limitations on microbes and thus increase the immobilization of N, which will reduce plant-available N, thereby restricting plant growth (Figure 6). This reduction in growth is hypothesized to last until the snags decompose (Figure 5). At this point, immobilized N from snag decomposition may become available to plants, leading to increases in plant growth, with perhaps higher productivity and leaf area as compared with pre-disturbed productivity (Edburg *et al.* 2011).

Recovery of net ecosystem productivity (NEP = 0) to steady-state conditions was hypothesized by Odum (1969), whereas Goulden *et al.* (2011) demonstrated that near-steady-state conditions were achieved about 150 years after fire in the boreal forests of northern Canada. We anticipate faster recovery rates following bark beetle disturbances for several reasons: the amount of tree mortality within a given location is often lower than for stand-replacing fires, in which the majority of trees are killed; in addition, bark beetles prefer larger host trees, leaving non-host trees, smaller diameter trees, or shrubby or herbaceous vegetation intact (Shore and Safranyik 1992). Thus, post-outbreak stands may include a considerable quantity of surviving vegetation that is able to take advantage of increased nutrients, light, and water, and so undergo rapidly increasing growth rates (Romme *et al.* 1986; Veblen *et al.* 1991; Brown *et al.* 2010; Pfeifer *et al.* 2011). Successional changes after bark beetle outbreaks (Veblen *et al.* 1991) may also play a key role in recovery
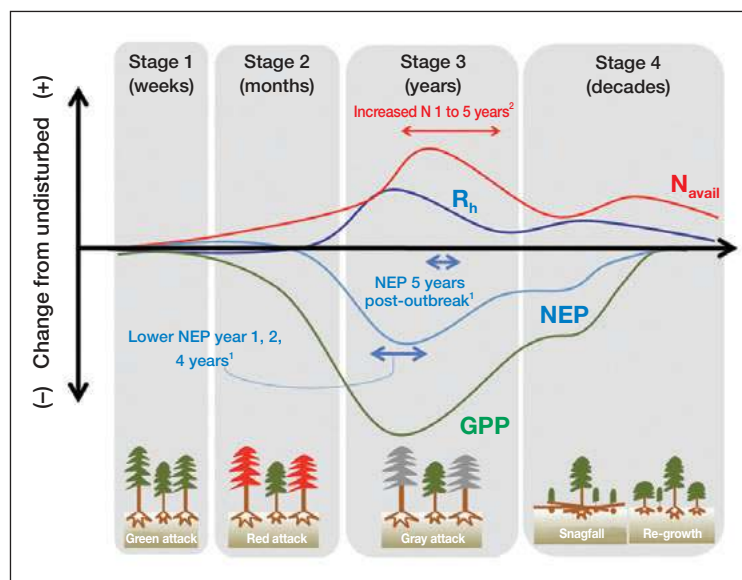
**Figure 6.** *Carbon and nutrient dynamics following a mountain pine beetle outbreak. $N_{avail}$ = available nutrients; GPP = gross primary productivity; $R_h$ (heterotrophic respiration) = decomposition; NEP = net ecosystem productivity. Lower NEP reported in years 1, 2, and 4 following a mountain pine beetle outbreak by [1]Brown* et al. *(2010). Near neutral NEP reported by Brown* et al. *(2010) in year 5. Increased soil mineral N reported in years 1–5 by [2]Huber (2005).*

to steady-state conditions and may result in substantially different ecosystem functioning as compared with the pre-outbreak forest. For example, water cycling in deciduous aspen (*Populus tremuloides*)-dominated ecosystems will be different than in lodgepole pine ecosystems (Fahey and Knight 1986).

■ **Management implications**

Primary management concerns fall into three categories: (1) fire risk, (2) water quantity and quality, and (3) regeneration of forest stands. First, fire hazard is the subject of a major public policy debate. Although often viewed by the public as increasing the probability and severity of fires, beetle-attacked stands progress through various canopy structure stages (ie green attack, red attack, gray attack, snagfall, and re-growth) that may lead to either enhancement or reduction of wildfire characteristics (Jenkins *et al.* 2008; Hicke *et al.* 2012). In British Columbia, salvage-logging efforts are being conducted to reduce fire hazards and to provide a positive economic benefit from forest products (Stinson *et al.* 2011). Understanding the impacts of this harvest on biogeophysical processes and biogeochemical cycles will help decision makers select post-outbreak management options. Second, water managers are faced with major uncertainties in water quantity and quality downstream of impacted watersheds. Addressing these impacts requires a coupled conceptual view similar to that presented here because the energy, water, C, and N cycles are intimately linked. Finally, the recovery of forested stands is important for the ecosystem services related to

water supply, C sequestration, wildlife habitat, and recreation. Knowledge about the timing of recovery through vegetation succession is needed to predict the timing of impacts on biogeophysical processes and biogeochemical cycles, and thus the timing of impacts on the aforementioned ecosystem services.

■ **Conclusions**

We face many challenges in testing and refining this conceptual framework of cascading ecosystem impacts of bark beetle-caused tree mortality. Evaluation of our framework requires datasets spanning the time frame of the cascading impacts (weeks to decades). We currently have only limited observational datasets that describe the location, severity, and duration of tree mortality. These dynamic processes must also be integrated into ecosystem models, which can then be evaluated against coordinated field observations. Long-term observational studies that span pre- and post-outbreak periods are the most useful because they capture the temporal dynamics needed for model evaluation. Amiro *et al.* (2010), for instance, synthesized a chronosequence of eddy covariance measurements for several disturbances; however, bark beetle outbreaks were poorly represented in this synthesis because of the difficulty in maintaining long-term studies, locating eddy covariance towers within potential outbreak areas, and using such towers in topographically complex and geographically remote areas.

Quantifying how changes in stand-scale processes alter biogeophysical and biogeochemical cycling at regional scales remains an open research question. At the small catchment scale, where affected host species comprise a large fraction of the catchment area, a reduction in transpiration can be expected to increase stream flow. However, at the regional scale, if additional unaffected stands are included, it is unclear whether canopy-scale impacts will have any notable effects. Stand-level productivity can be substantially reduced following a severe bark beetle outbreak, suggesting that regional impacts occur as a result of severe outbreaks (eg the mountain pine beetle attack in British Columbia; Kurz *et al.* 2008). However, other regional occurrences are not as severe as that in British Columbia (Pfeifer *et al.* 2011), and the consequences of regional-scale events in North America may depend on the duration, size, and severity of attacks. Furthermore, it is unknown how impacts on biogeophysics and biogeochemistry from severe bark beetle outbreaks compare to other forcing signals, such as those associated with annual climate variability. Several key research themes that should be addressed in the future are:
- resolve tree mortality mechanisms caused by bark beetles and associated blue stain fungi;

- characterize how changes in soil moisture alter the coupling between biogeophysical and biogeochemical processes, including vertical and lateral moisture distribution;
- characterize and quantify site dependency of soil microbial feedbacks and the response of surviving trees and understory vegetation, including the potential export of nutrients;
- quantify the spatial extent and severity of outbreaks at watershed to regional scales;
- quantify changes in biogeochemical cycling across a wide range of spatial and temporal scales at sites with different successional trajectories; and
- isolate (or at least more clearly attribute) beetle-driven changes in ecosystem-scale water, energy, and biogeochemical budgets from those driven by natural climate variability and long-term climate and ecosystem trends.

In our opinion, addressing the aforementioned research themes will increase the understanding of the coupled biogeophysical and biogeochemical impacts of bark beetle outbreaks and lead to improved pre- and post-disturbance management decisions.

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