Comments

Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment

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Simard et al. (2011) have produced a comprehensive data set and analysis concerning mountain pine beetle (MPB; *Dendroctonus ponderosae*)-caused mortality and associated crown fire feedbacks in lodgepole pine (*Pinus contorta*)-dominated forests. Misapplication of the NEXUS fire modeling system (Scott and Reinhardt 2001) results in the suspect conclusion that active crown fire (perpetuation of flames through the canopy) probability is reduced in all post-mortality stages. Simard et al. (2011) assert that the loss of canopy fuel following tree mortality overwhelms the concomitant loss of foliar moisture content (FMC) but do not fully account for this drop in moisture or the resulting increase in surface fuels. Here, we show how to account for decreases in FMC and increases in surface fuels within NEXUS and report findings contrary to Simard et al.'s (2011) conclusions for the red stage (dead needles still within canopy). Overall, NEXUS is a questionable choice for this research due to its inherent lack of crown fire predictive capability (Cruz and Alexander 2010) and empirically derived crown fire models developed using living canopies (Van Wagner 1977, Rothermel 1991, Scott and Reinhardt 2001).

NEXUS and related fire modeling systems (e.g., FARSITE, FlamMap, BehavePlus, and FFE-FVS) rely on the integration of Rothermel's (1972) surface and crown (1991) fire spread models with Van Wagner's (1977, 1993) crown fire transition and propagation models (Scott 2006, Cruz and Alexander 2010). The fire modeling community recognizes the need for calibration of model input variables and parameters, including custom surface fuel models, which Simard et al. (2011) employ, to achieve accurate representations of observed, and thus predicted,

fire behavior. Without calibration, quantitative fire behavior output values can be wildly unrealistic, as large under-prediction biases are prevalent (Cruz and Alexander 2010). For example, necessitating 1000 km/h wind speeds to initiate crown fire in undisturbed lodgepole pine forests (Simard et al. 2011). However, relative comparisons of disturbed and undisturbed forests' fire behavior are possible when full consideration is given to the primary drivers of fire behavior.

Accounting for decreases in foliar moisture content

Fuel moisture content is a key driver of fire behavior due to water's energy absorption when converting thermal to latent heat (Rothermel 1972, Anderson 1982). Van Wagner (1989) incorporated changing FMC into his passive and active crown fire initiation and spread rate models with the use of foliar moisture effect (FME), which accounts for expected effects of moisture loss or gain on aerial flame radiation intensity (numerator) and heat of ignition (denominator):

$$\text{FME} = \frac{1000(1.5 - 0.00275\text{FMC})^4}{460 + 25.9\text{FMC}}. \quad (1)$$

Here, FMC is the weighted average of foliar moisture content expressed as a percent of dry biomass. FME is normalized using a standard FMC (FME_0), usually 100% (Scott and Reinhardt 2001). The resulting potential active crown fire rate of spread (RSC_f) is a function of the crown fire spread rate (RSC), as per Van Wagner (1977), modified by the normalized FME (FME/FME_0):

$$\text{RSC}_f = \text{RSC}\left(\frac{\text{FME}}{\text{FME}_0}\right). \quad (2)$$

In NEXUS, however, RSC_f has been replaced by Rothermel's (1991) crown fire model, which was empirically derived from observations of seven crown fires, outputs from Rothermel's (1972) surface fire spread model using constant fuel loadings (R), and a constant wind reduction factor of 0.4:

$$\text{RSC}_f = 3.34R_{0.4}. \quad (3)$$

For MPB-killed canopies, this substitution is fundamentally flawed because Rothermel's (1991) model assumes all crown fires occur in live fuels exhibiting spread rates similar to observed wildfires, without accounting for changes in FMC or other canopy variables. Therefore, Simard et al.'s (2011) analysis does not account for reduced FMC and other changing canopy fuel variable effects on active crown fire spread rates. Recognizing this limitation, NEXUS' creators provided an FME correction option for Rothermel's (1991) derivation of

RSC$_f$ (Scott and Reinhardt 2001). Applying this FME correction for Simard et al.'s (2011) asserted 63% red-needle stage FMC causes potential active crown fire spread rates to increase by a factor of about two.

The potential active crown fire spread rate problems propagate into estimates of active crown fire initiation probability as well. In this case, NEXUS incorporates canopy fuel losses from needle drop but does not account for the concomitant FMC reduction, yielding a large under-prediction bias. Initiation thresholds correspond to a minimum active crown fire spread rate (RAC), determined by crown bulk density (CBD) of available fuel, and the critical mass flow rate for solid crown flame (S; Van Wagner 1977):

$$RAC = \frac{S}{CBD}. \qquad (4)$$

NEXUS compares RSC$_f$ directly to RAC, initiating active crown fire when RSC$_f \geq$ RAC (Scott 2006). A 50% drop in CBD (Simard et al. 2011) effectively increases RAC by a factor of two, while the aforementioned application of FME raises RSC$_f$ by the same amount, yielding virtually no change in active crown fire initiation probability.

FME use was not explored by Simard et al. (2011), leading to the unfounded conclusion that "canopy moisture in fire behavior models has a relatively small effect compared to other variables." If properly accounted for, reduced FMC drastically increases crown fire spread rates. The exponential relationship between FMC and potential active crown fire spread and initiation probability implies that crown fire behavior would be substantially worse in forest stands with greater mortality than those sampled (36–82%, mean 58%) by Simard et al. (2011), often reaching 90% mortality for larger trees on a landscape scale (Raffa et al. 2008). Although FME has not been experimentally validated and large uncertainties concerning the effect of FMC on fire behavior still exist (Van Wagner 1998, Cruz et al. 2005), it is the only variable within NEXUS that can account for the crucial drop in FMC and related active crown fire behavior in MPB-affected forests.

Accounting for increases in surface fuels

Simard et al. (2011) report a 40% loss in canopy fuels but do not account for the associated increase in surface fuels from the falling needles in their models. Despite measuring a statistically significant 60% increase in needle litter depth in red-stage surface fuels, these fuels were not incorporated into the custom fuel models for the stated reason that "this variable does not contribute to surface fire spread in fire behavior models." Fine fuels (<0.6 cm diameter) are, in fact, the most significant fuel class contributing to the flaming front of a fire (Rothermel 1972), and many standard surface fuel models reflect this (Anderson 1982, Scott and Burgan 2005), including fuel model 10, "timber litter and understory" from which Simard et al. (2011) derived their custom fuel models. Given a bulk density estimation of 42.1 kg/m^3 for intermediate-length need litter (Brown 1981), a 60% increase in needle litter depth equates to a 4.21 Mg/ha increase in fine fuels. When accounting for these increased needle litter fuels in disturbed forest custom fuel models, NEXUS predicts a 23% increase in surface fireline intensity under Simard et al.'s (2011) defined extreme weather conditions, exacerbating surface fire spread rates and crown fire initiation probability.

Conclusion

Bark-beetle-caused tree mortality affects 47 million hectares of western North American forests (Raffa et al. 2008), an area larger than California that continues to increase. Studies such as Simard et al. (2011) may influence how these vast tracts of land are managed. Canopy fuel and moisture loss dynamics and associated surface fuel increases must be properly accounted for before reliable conclusions about crown fire feedbacks in beetle-killed forests can be reached. Even if these dynamics are fully considered in the NEXUS fire modeling system, the techniques push well beyond the model application bounds, which are based solely on living canopies (Cruz and Alexander 2010). MPB epidemics change not only crown fire behavior but surface, ground, and spot fire frequency and intensity as well, creating ecological, land management, and fire suppression implications that need consideration. Future studies of this important forest disturbance should seek to characterize the cumulative, spatiotemporal feedbacks that MPB-caused tree mortality has on all aspects of fire behavior.

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Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment

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An expansive mountain pine beetle (MPB) epidemic is currently impacting North American forests (Raffa et al. 2008). As beetle-attacked trees die, lose their needles, and eventually fall to the ground, there are substantial changes in stand structure. These fuel changes likely affect both surface and crown fire behavior, but there is not yet a consensus among experts regarding the nature and magnitude of these effects (Jenkins et al. 2008). Simard et al. (2011; hereafter referred to as SRGT) used linked crown fire models implemented in the NEXUS crown fire modeling system (Scott and Reinhardt 2001) to predict the occurrence of active crown fire across a chronosequence of increasing time since attack. They concluded that, under moderate fire weather conditions, recently attacked or red-stage stands had a lower occurrence of active crown fire than undisturbed stands. Here, we suggest that these conclusions are compromised because (1) the fire behavior modeling framework used has no mechanisms for considering highly heterogeneous fuels and (2) their use of this framework omitted critical aspects of how canopy and surface fuels change after an attack, particularly during the first two to three years.

Fire behavior modeling framework used was poorly suited to address MPB-wildfire interactions.—The NEXUS (Scott 1999, Scott and Reinhardt 2001) crown fire behavior modeling system calculates the occurrence of active crown fire by linking predictive models of surface fire spread and intensity (Rothermel 1972), crown fire initiation (Van Wagner 1977), and crown fire spread (Rothermel 1991). For the purposes of further discussion, we will refer to this collection of models as the linked crown fire model. It is important to note that these models are also implemented in a number of fire behavior modeling systems, such as the point-based BehavePlus fire modeling system (Andrews et al. 2008) or spatial fire behavior prediction systems such as FARSITE (Finney 2004), FlamMap (Finney 2002), and FVS-FFE (Rebain et al. 2010), and thus our discussions here are not limited to only NEXUS but rather, apply to the entire suite of fire modeling applications that implement these models. These systems are commonly used to support fire management decisions throughout the United States. To understand why these crown fire models may not accurately predict crown fire behavior in MPB attacked stands, some background into their components and the linkages between them is necessary.

These linked models predict active crown fire occurrence in two stages: (1) initiation, in which the fire ascends from the surface into tree crowns, and (2) spread, in which the fire is carried through the canopy. Surface fire intensity is simulated by the Rothermel surface fire spread model (Rothermel 1972), and crown fire spread rate is simulated by the Rothermel crown fire

spread rate model (Rothermel 1991), which is based on a correlation with the surface spread model. For crown fire initiation, surface fire intensity must surpass the model-predicted critical surface fire intensity threshold, which is determined by foliar moisture content (FMC) and effective canopy base height (CBH). When FMC or CBH values are large, higher surface fire intensities are required for crown fire initiation. Active crown fire spread occurs when the model-predicted crown fire spread rate exceeds the critical crown fire rate of spread threshold predicted by the Van Wagner model. Critical crown fire rate of spread is determined solely by canopy bulk density (CBD) or the amount of dry foliar biomass per unit volume of canopy. Critical crown fire rate of spread is sensitive to small changes in CBD, particularly when CBD is below ~ 0.16 kg/m^3 (Fig. 1A).

Despite a legacy of fire behavior model use, and reliance on them for fire management decision making, there is growing recognition that crown fires are not well modeled by these existing linked model systems and that crown fires in general are poorly understood (see review by Cruz and Alexander [2010]). Additionally, it is recognized that these models are biased toward under-predicting the occurrence of active crown fires (Cruz and Alexander 2010). The fire spread model assumes homogenous, continuous fuels and steady-state flame spread, and these assumptions are inconsistent with the characteristics associated with actively spreading crown fires (Cohen et al. 2006, Finney et al. 2010). Fuel and flame spread assumptions of the fire models are even less applicable to beetle-killed stands, where the mixture of live and dead trees produces substantial spatial variability in fuel continuity, homogeneity, and moisture content. In recently beetle-killed stands, the red-needled foliage has low FMC values, which are far below the empirical data range used by the Van Wagner model (1977). Recognizing that these fire behavior models are likely mischaracterizing expected fire behavior in beetle-killed stands, it should be concluded that simulation results must be interpreted with caution.

Our two principal concerns with SRGT's use and interpretation of the linked crown fire models to predict active crown fire occurrence in beetle-killed stands are that their approach omitted critical aspects of how beetle attacks predictably alter surface and canopy fuels and that they interpreted model outputs without regard to the model's sensitivity to their choice of inputs. We demonstrate throughout the rest of this paper how model predictions and SRGT's conclusions may have been different had they considered the full range of surface and fuel structure changes that occur after a mountain pine beetle attack.

Critical aspects of canopy and surface fuel changes were omitted for stands recently attacked by MPB.— Choosing the linked crown fire models as a fire modeling

platform forced SRGT to make several assumptions about crown fuel dynamics following a beetle attack and these assumptions led to significant under-predictions of crown fire potential in red-stage stands. SRGT estimated crown foliar biomass for all trees, regardless of attack condition, using common allometric equations that relate tree diameter to foliar biomass. All red-needle trees were classified into two categories based on having more than or less than 50% of their original foliage remaining and then each tree's foliar biomass was reduced by 25% and 75% for the two foliar categories, respectively (see SRGT: 9). The modified crown biomass values were then used to estimate stand-level CBD. By applying a subjective biomass reduction to all red-needle trees, SRGT failed to account for stands with trees retaining most of their red needles. This early stage of attack where CBD remains unchanged and the foliar moisture of the trees declines rapidly represents a critical reference point when evaluating the impacts of fuel changes on crown fire potential (Fig. 1C). While foliar biomass loss is expected in beetle-killed trees, this reduction is not instantaneous and needles remain attached for up to three years after an MPB attack (British Columbia Ministry of Forests 1995). Though no research currently exists to show the timing of needle loss after an attack, it is reasonable to assume that most needles are retained for up to two years after an attack and then gradually lost over time until there are no needles remaining on the trees after the third year. These reductions in crown needle biomass would effect a continuous reduction of crown fire potential as an attack progresses rather than an instantaneous or discrete shift from one state (full needle retention) to another (25% or 75% needle loss). Thus, crown fire potential will be highest when needles are dessicated but not lost from the tree and then it will likely decrease as needles fall. The latter case would more closely match predictions made by SRGT, but the former case is the point in the post-attack time sequence where stands would have the highest active crown fire potential.

SRGT's average CBD of 0.16 kg/m^3 for undisturbed stands (estimated from SRGT: Fig. 6D) falls within a region of the crown fire model where small reductions in CBD correspond to large increases in predicted critical crown fire rate of spread (Fig. 1A). A 50% CBD reduction from this value corresponds to a doubling of the critical crown fire rate of spread criteria. Proper characterization of stand CBD is critical to correctly assess that stand's active crown fire potential. SRGT's categorical reduction of foliar biomass greatly reduced their calculated CBD values (0.07 kg/m^3 on average) and consequently reduced model-predicted active crown fire potential for any stand with red needle trees.

Foliar biomass reductions also influenced the canopy-average FMC values applied by SRGT. In a given stand,
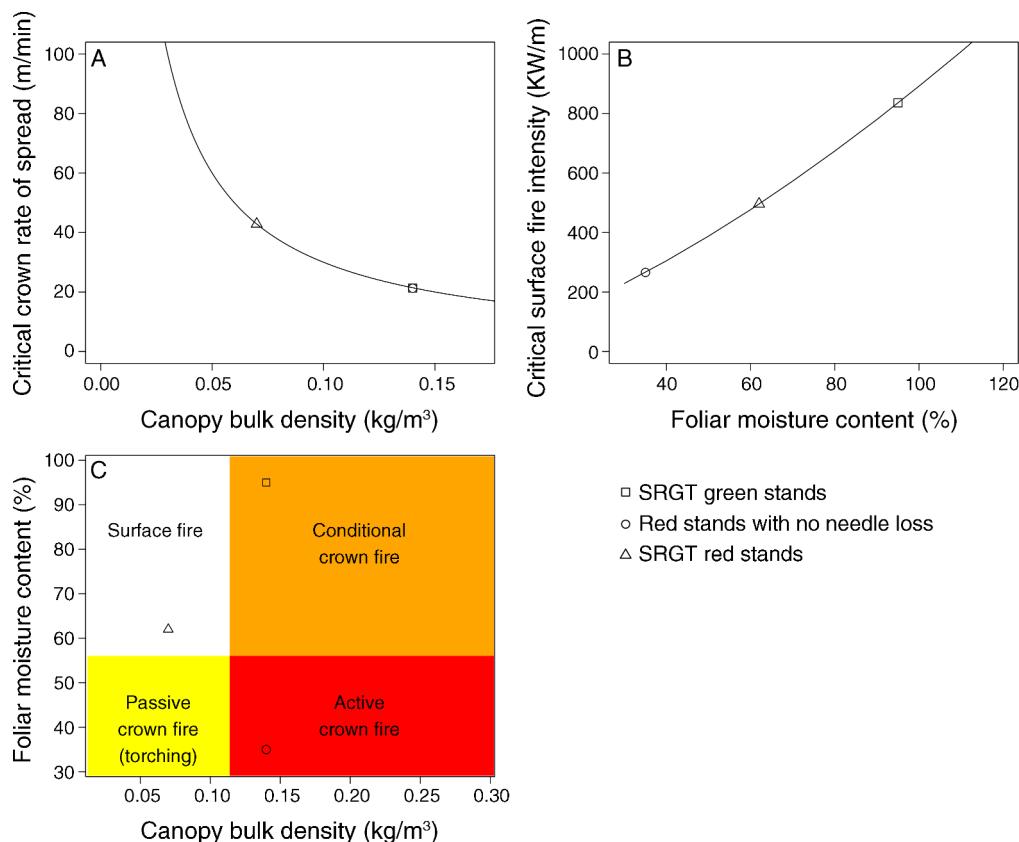
FIG. 1.   Relationships between canopy bulk density (CBD), foliar moisture content (FMC), and crown fire criteria/potential (Van Wagner 1977). The square symbol shows the model predictions for a typical SRGT (short for Simard et al. [2011]) green stand with a crown bulk density of 0.16 kg/m^3 and an FMC of 95%. The triangle symbol shows a typical SRGT red-needle stand (CBD = 0.07 kg/m^3, FMC = 63%). The open circle illustrates the case where an appropriately low FMC is used (35%) but no needles have fallen from the tree and thus CBD has not yet been reduced (CBD = 0.16 kg/m^3). Panel A shows the sensitivity of critical crown fire spread rates to changes in CBD, indicating that as CBD decreases from 0.16 kg/m^3 to 0.07 kg/m^3, the criteria for active crown fire doubles. Panel B shows the sensitivity of critical surface fire intensity to changes in FMC, and it shows that, as FMC increases (from 63% to 95%), the crown fire initiation criteria nearly triples. Panel C shows that the model consistently predicts active crown fire if one considers a stand where attacked needles have a low FMC and yet have not lost needles (CBD is unchanged). (See Appendix A for more details.)

they used a foliar biomass-weighted average of green and red needle FMC as a linked crown fire model input. When low FMC, red-needle foliar biomass is reduced, a larger proportion of the needles in a given stand are high FMC, green needles. This would overestimate the canopy-average FMC. The lowest canopy-average FMC used by SRGT was 63% (see SRGT:14), which is more than 10 times the moisture content of red needles (as reported in SRGT: Table 2). While this simplification was required because the linked crown fire models only allow a single FMC input for a given stand, this simple averaging is unjustified, given the bimodal nature of green and red needle FMC. These uncharacteristically high FMC values would have erroneously suggested a reduction in the surface-to-crown transition potential of attacked stands relative to what might be expected for trees with very low foliar moisture contents. In recent

years, more detailed physics-based fire models have emerged, such as FIRETEC (Linn et al. 2002, 2005) and the Wildland–Urban Interface Fire Dynamics Simulator (WFDS; Mell et al. 2009) in which individual beetle-killed trees and healthy trees could have different fuel moistures, and fire behavior is sensitive to the geometry and arrangement of the fuel. The substantially higher detail with which both fuels and the physical processes of fire are represented in these models makes them more appropriate than the linked crown fire models used by SRGT when simulating fire behavior in highly hetero-geneous, beetle-kill fuels.

Ultimately, inaccurate and insufficient characteriza-tion of the full range of foliar biomass possibilities following a MPB attack produced inaccurate CBD and FMC model inputs and an unrealistic decrease in the active crown fire potential of red-needle stands. Using

more representative CBD and conservative FMC values for red-stage stands in the early stages of beetle attacks (FMC = 35% and CBD = 0.016 kg/m^3, as denoted by open circles in Fig. 1), we found that the model predicts an active crown fire (Fig. 1C). In fact, we found that any stand with a canopy-average foliar moisture content below ~75% and a CBD above 0.09 kg/m^3 would support an actively spreading crown fire under the same environmental conditions used by SRGT (Fig. 1C). The failure by SRGT to recognize, account for, and appropriately characterize expected changes in CBD and FMC in the first two to three years following a MPB attack led to an under-prediction of crown fire potential.

SRGT's assumptions associated with surface fuel characterization also omitted key changes associated with beetle attacks, which reduced the chance of predicting active crown fire potential. In the linked crown fire models modeling system, surface fuels influence crown fire potential by influencing surface fire intensity, which must exceed a critical value for crown fire initiation to occur. Although they reported significant increases in litter depth between undisturbed and red-stage stands, these fuel changes were not included in the custom surface fuel models used by SRGT in their fire behavior calculations. Assuming a litter bulk density of 11 kg/m^3 (consistent with reported literature [Brown 1981]), and the average litter depths reported in undisturbed (1.6 cm), red-stage (2.6 cm), and gray-stage (2.3 cm) stands, 1-hour fuel loads would increase by 1.76, 2.86, and 2.31 Mg/ha, respectively, in beetle-killed stands.

When we compared model-predicted surface fire intensities under SRGT's dry summer fuel moisture and open wind (20 km/h) scenario with and without litter included in the 1-hour fuel category, the incorporation of litter increased model-predicted surface fire intensities by 78%, 85%, and 95% for undisturbed, red-stage stands, and gray-stage stands, respectively (see Appendix B: Table B2). Increased surface fire intensities, as result of including litter as fine dead surface fuels, would increase surface fire intensity and thus would increase predicted crown fire initiation.

Space-for-time chronosequence sampling introduced fuels variability and resulted in an incomplete characterization of fuel changes that occur as time since MPB attack increases.—With the exception of an increase in litter depth between undisturbed and red-stage stands, SRGT found no significant changes in any surface fuel category over the time-since-beetle attack chronosequence. We suggest that the lack of significant surface fuel changes reflects the high variability introduced by sampling stands along a space-for-time chronosequence, rather than inconsequential changes over time in a given location as SRGT suggests.

If individual trees and their immediate surroundings were monitored over time following an attack, a very predictable sequence of events would be observed, with needles falling after two to three years, followed by twigs, branches, and eventually large branches and tree trunks. This shedding of canopy fuels to the forest floor would increase surface fuel loads, particularly in the early years following a beetle attack. Beyond the initial years following beetle attacks, however, potential decomposition losses and rates are highly influenced by species characteristics (Cornwell et al. 2008) and biophysical setting (Keane 2008). Smaller diameter fuel components have faster decay rates (Keane 2008) and thus are less persistent over time.

In the SRGT study, expected patterns of surface fuel recruitment are not recognized. Significant losses in canopy fuels (SRGT: Fig. 6D and E) are not matched by increases in surface fuels (SRGT: Fig. 4), so some fuel components appear to vanish over time. Surface fuel abundance was not found to be significantly different between attacked and undisturbed stands (SRGT: Fig. 4B, C, D, and G). One potential explanation for the missing fuels is the intrinsic high variability in surface fuels (Woldendorp et al. 2004). High variability is problematic for fuels sampling in general; accuracy assessment studies of commonly used line intercept methods, such as those employed in this study, demonstrated that transect lengths must be an order of magnitude longer (>1000 m) than those employed by SRGT (100 m) in order to achieve confidence intervals below 25% (Pickford and Hazard 1978, Sikkink and Keane 2008). Shorter lengths may be adequate for litter (Sikkink and Keane 2008), which may explain why this variable alone was significant in SRGT's study. This high variability could result in significant inaccuracy in SRGT's fuel quantity estimates, which could substantially obscure effects over time, even if they had sampled the same stands over time. Additional issues likely arise from pitfalls associated with chronosequence sampling approaches, which include blurring small-scale heterogeneity by seeking plot-scale homogeneity or magnifying inherent site differences across heterogeneous space (Pickett 1989). Increasing surface fuel variability beyond what is already an intrinsic component of surface fuels could have resulted in substantial inaccuracy in SRGT's surface fuel load estimates and obscured fuel changes over time.

Conclusion

A robust understanding of the nature of fuel and fire behavior changes over time following beetle attack is essential for fire management, risk assessments, and successful long-term ecosystem management. Conclusions reported by SRGT, however, obscure our understanding of these changes because they fail to capture critical surface and crown fuel changes as a MPB attack progresses through a given stand. Use of a fire behavior

modeling framework that has no mechanism for considering highly heterogeneous fuels, omission of critical canopy and surface fuel changes in stands attacked by MPB, and potential increases in the inherent variability associated with fuels sampling in general and along a chronosequence, led to the predicted reduction in the crown fire potential in red-needle stands under the moderate conditions reported by SRGT. As we have demonstrated, if SRGT had chosen estimates of surface and canopy fuel inputs that better described stands during the early stages of a MPB attack, inevitably they would have found an increase in predicted crown fire potential in almost all cases, particularly during the first three years after an attack (Fig. 1C).

As the MPB epidemic continues in fire-prone North American forests, the scientific community must quantify expected changes in fire behavior in a manner that increases the understanding of pathogen and fire interactions. Some form of fire modeling will be associated with these studies. However, these models should be evaluated against observed fire behavior when possible (Alexander and Cruz 2006). In the absence of field-based fire behavior observations, fire models still play a role in predicting the potential impacts of any type of fuel modifications on expected fire behavior. However, great care is needed when choosing model inputs and evaluating model outputs, and the reliability and limitations of fire behavior model predictions must always be considered and explicitly discussed when reporting simulation results.

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Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Reply

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In a recent paper, we showed that contrary to conventional wisdom, outbreaks of the mountain pine beetle (*Dendroctonus ponderosae*) did not increase the predicted potential for active crown fires relative to comparable undisturbed stands in lodgepole pine (*Pinus contorta* var. *latifolia*) forests of Greater Yellowstone (Simard et al. 2011). Under certain intermediate weather conditions, the potential for active crown fires was actually predicted to decrease relative to comparable stands undisturbed by bark beetles. Our study was based on a rich data set of forest fuels sampled in a robust post-outbreak chronosequence of beetle-killed and undisturbed stands that were replicated in space and time and validated with dendrochronological reconstructions of pre-outbreak conditions. Moran and Cochrane (2012) and Jolly et al. (2012) have expressed concerns about certain aspects of our fire behavior modeling in recently killed stands. Although these authors do not refute the conclusions of our study, they do raise issues that are

highly debated among scientists and practitioners alike. Here we explain that these concerns are largely based on misconceptions about the dynamics of mountain pine beetle (MPB) outbreaks, and we provide complementary data that strengthen our conclusions.

Three misconceptions

Severity of beetle-caused tree mortality.—A first misconception about MPB outbreak dynamics by Jolly et al. (2012) and Moran and Cochrane (2012) is that many lodgepole pine forests attacked by the MPB sustain extremely high mortality—sometimes up to 100% of the basal area or number of trees within a stand—and that such areas of extremely high mortality are common across the landscape. Surprisingly, given how conspicuous beetle-killed trees are in affected landscapes, this notion is rarely substantiated by quantitative data. Mortality of 100% may be observed at very fine scales (a few square meters) but is rarely observed at scales > 1 ha (Rocca and Romme 2009), which are the scales relevant to consideration of fire behavior. In British Columbia, aerial surveys of the MPB outbreak, which peaked in 2005 and is now receding, show that cumulative (1999–2010) mortality of 100% (at a spatial resolution of 16 ha) is observed in <1% of the affected area, and mortality levels > 85% occurred on only 5% of the affected landscape (Walton 2011). Similarly, after reviewing published studies from the U.S. Rocky Mountains, we were unable to find study sites that sustained more than 85% mortality, either on a tree density or a basal area basis (Roe and Amman 1970, Amman and Baker 1972, Amman et al. 1973, Klutsch et al. 2009, Collins et al. 2010, 2011, Diskin et al. 2011). A corollary of these results is that the mortality levels of the stands that we studied (up to 82% basal area beetle killed) are within the range of mortality observed in 95% of MPB-affected areas.

Timing of beetle-caused tree mortality.—A second misconception evident in both comments is that infestations within a given stand occur over such a short period of time that beetle-caused tree mortality is synchronous. On the contrary, MPB infestations develop gradually, typically over several years, and tree mortality for any given year is always considerably less than the total mortality accumulated over the course of the outbreak. Data from the British Columbia outbreak (1999–2010) showed that annual mortality was >50% on <5% of the affected area during nearly the entire

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outbreak. An exception occurred at the peak of the outbreak (2005, with >8.7 million hectares affected), when >50% mortality was observed on 10% of the affected area (Westfall 2006). In other words, for any given year during the outbreak, severe mortality (>50%) was observed on an extremely small fraction of the landscape.

The consequence of these two aspects of MPB outbreak dynamics is that only a fraction of trees die every year during an outbreak. Mortality is spread out over several years, and as new trees get attacked and their needles turn red, previously killed red trees progressively lose their needles. At the beginning of a local infestation, there are probably one or two years during which stand-level foliar moisture decreases but canopy biomass does not because new trees are killed but none of them lose their needles. However, tree mortality in these first years of attack is usually very low because beetle populations are building up slowly; therefore the stand-level decrease in foliar moisture is probably also very small because the dead trees make up a small fraction of the stands. After this very short period of time however (1–2 years), these first beetle-killed trees start losing their needles and canopy fuel loads are reduced. Because of the slow and partial effect of the beetles, it would be extremely rare for all trees in a stand to be in the "red" stage during any single year, and indeed, we have never observed this in the field. Individual trees go through a definite red stage where most of the needles are dry but still in the canopy (the year after beetle attack); however, at the stand level, there is always a mixture of green (unattacked), red, and gray trees (no needles left in the canopy). MPB-affected stands are often classified in the so-called red and gray stages based on relative prevalence, including in our study, because this is a convenient and conceptually straightforward way to describe the different phases of MPB infestation; however, there is no such thing as a fully red-stage stand. These points, which were discussed in our paper, explain why stands in the "red stage" in our study had already lost canopy fuels (Simard et al. 2011: Fig. 6). Based on these facts, it becomes clear that the "Red stands with no needle loss" depicted in Jolly et al. (2012): Fig. 1 are rarely, if ever, observed in the field. Representing the average red-needle stage as a stand with 100% mortality and 100% dead needle retention is misleading, and modeling results based on such values are unrealistic and do not refute our interpretations.

Low canopy fuel loads in the red-stage stands that we studied were not, as Jolly et al. speculate, caused by an underestimation of the mass of dead needles. We classified the amount of red needles on individual trees in three categories (0–5% on either live or dead trees, 6–50% and 51–100% on dead trees) and then we used the mid-point of these classes (0%, 25%, and 75%) to determine the proportion of red needles left on the trees and to determine the total mass of red needles. Using the mid-point of the classes to convert the categories to a single number is a standard approach and does not introduce a systematic bias: it can either overpredict or underpredict needle abundance for individual trees. We did not encounter stands where all the red trees retained 100% of their needles, so there is no reason to think that there was an underprediction in red-stage stands. The quantification of needle abundance in 0% vs. 25% vs. 75% were done at the tree level, and then integrated at the stand level, which is the level of analysis that we used for determining total canopy fuel load and weighted foliar moisture. Consequently, the stand-level values of needle abundance can take any value and represent a continuum, contrary to what Jolly et al. assert.

Accumulation of fine surface fuels.—The third misconception by Jolly et al. (2012) and Moran and Cochrane (2012) is that all canopy fuels that fall to the ground should be reflected in surface accumulation over the period of the outbreak. This assumption is incorrect because it fails to account for the gradual input of needle litter over several years and the key role of litter decomposition during that time period. Because MPB infestations are a slow and partial disturbance, canopy fuels fall to the ground over several years. The ongoing decomposition of fresh and old litter explains why litter mass does not show a pulse that is commensurate with the decline in canopy fuels and also explains why some fuel components seem to (and do) vanish over time. Also, because the density of fresh litter is lower than that of older litter, there can be a post-outbreak increase in litter depth without a similar increase in litter mass. We observed this trend in our data: in the first few post-outbreak years, litter depth increased because of the addition of new, looser material, but litter mass did not change (Griffin et al. 2011) because of the concurrent decomposition of old and fresh material.

As a proof of concept, we use our field data (Griffin et al. 2011) and decomposition rates from the literature to ask whether decomposition could explain why the increase in litter mass after four years was less than the mass of canopy fuels lost during the same period of time. The field data presented in Griffin et al. (2011) come from the same chronosequence used in Simard et al. (2011) but include litter mass data, which were not reported in Simard et al. (2011). We use the average foliar biomass values of undisturbed (year 0; 1107 g/m^2) and gray-stage stands (year 4; 358 g/m^2) to determine the average foliar biomass lost in four years (749 g/m^2). Then we can add this foliar biomass to the litter mass (1512 g/m^2) measured on the floor of the undisturbed stands. If all the foliar biomass fell and did not decompose, we should expect a total of 2261 g/m^2 of litter in gray-stage stands; instead, we measured 2010 g/m^2 (Griffin et al. 2011). Annual mass loss rates of newly fallen pine needle litter in the Rocky Mountain

region are estimated to be 10–20% in the first two years and about 5% thereafter (Yavitt and Fahey 1986, Taylor et al. 1991, Remsburg and Turner 2006, Keane 2008*a*, *b*, Chatterjee et al. 2009). If we use conservative decay rates from the literature (15% mass loss in fresh litter, 10% mass loss in one-year-old litter, and 5% annual mass loss for older material), we see that litter mass in gray-stage stands would never exceed 2000 g/m^2, in accordance with our field data. These results are surprisingly robust to different temporal patterns of needle fall. This exercise demonstrates that litter decomposition can explain the lack of response of litter mass to the input of foliar biomass caused by the MPB infestation. This exercise also demonstrates that within a modeling environment, it is inappropriate and ecologically unrealistic to convert all foliar biomass from beetle-killed trees into accumulated surface litter.

The failure of Moran and Cochrane and Jolly et al. to recognize and account for the slow and partial nature of MPB infestations and for the key role of litter decomposition led to the erroneous conclusions that (1) red-stage stands all have a very high proportion of dead trees retaining 100% of their dead needles, resulting in stand-level canopy fuel moisture content as low as 35% (Jolly et al. 2012: Fig. 1); (2) that this dead foliage would fall in a large, relatively synchronous pulse; and (3) that needle input would greatly increase litter mass in red and gray-stage stands. Consequently, the modeling results derived from these inflated canopy and surface fuel load values are unrealistic and do not refute our findings.

Canopy moisture and fire behavior

Linked crown fire models, including NEXUS (Scott and Reinhardt 2001) but also other modeling systems like BehavePlus, FVS-FFE, FARSITE, and FlamMap (Scott 2006), use a stand-level average foliar moisture content, which, to the best of our knowledge, is not incompatible with the bimodal distribution of foliar moisture content in beetle-affected stands. Our use of a biomass-weighted average foliar moisture is appropriate and has been used by Van Wagner himself, who combined foliar moisture content values of 82.0% to 111.5% for live trees with moisture content values of 9% for fine dead twigs in pine crowns to predict crown fire behavior in jack pine stands (Van Wagner 1993). The effect of foliar moisture on crown fire behavior is uncertain, and several analyses of experimental fire data did not find a detectable effect of foliar moisture (over a range of 75–168%) on the initiation of crowning or on crown fire spread (Van Wagner 1998, Cruz et al. 2004, 2005, 2006). Van Wagner developed the foliar moisture effect (FME) to include the theoretical effect of foliar moisture content (Van Wagner 1989) but subsequently removed it from the Canadian Forest Fire Behavior Prediction System (CFFBPS; Forestry Canada Fire Danger Group 1992:17) for all fuel types (which include

mature (C-3) and immature (C-4) jack pine or lodgepole pine) except for fuel type C-6, conifer plantation. The FME was removed because an analysis of the fire data in the CFFBPS database failed to find an effect of foliar moisture on crown fire rate of spread and because it never had (and still never has) been tested empirically (Forestry Canada Fire Danger Group 1992, Van Wagner 1998). The performance of the FME is thus completely unknown, which probably explains why it has never been used in practice. Given the unreliable nature of the FME, it is questionable that its use, as suggested by Moran and Cochrane (2012), would give any valid results. However, if the FME correction turned out to be valid, then according to Moran and Cochrane's calculations, the effect of lower moisture in red-stage stands would be cancelled by the reduction in canopy fuels, thus making red-stage stands no more likely to exhibit active crown fire behavior than comparable undisturbed stands. These results, if valid, would then be in accordance with our general conclusion that MPB infestations do not increase the potential for active crown fires compared to stands that were not disturbed by MPB.

Chronosequence approach

Short of having long-term monitoring data, the chronosequence approach is the best way to study secondary forest succession. The validity of a post-disturbance chronosequence is based on the assumption that all study sites have similar site conditions, that the forest stands were similar before the disturbance, and that disturbance severity was the same in all disturbed plots, but these assumptions are rarely verified (Johnson and Miyanishi 2008). On the contrary, our post-outbreak chronosequence was rigorously validated by reconstructing pre-outbreak conditions and disturbance severity using dendrochronology, and replicated in space (several replicates for each time-since-beetle class) and time (two independent sampling campaigns: 1981 and 2007), making it one of the most robust and replicated post-disturbance chronosequences in the ecological literature (see also Lecomte et al. 2005, Simard et al. 2007). The two independent sampling periods (1981 and 2007) show the same temporal trends in the amount of surface fuels, demonstrating the temporal stationarity of the chronosequence. Jolly et al.'s assertion that the variability induced by the chronosequence approach masked the effects of the beetle outbreak on the forest fuels is speculative, and no evidence is provided to support this allegation. On the contrary, we note that the surface fuel data presented in Simard et al. (2011) show a remarkably low variability within the undisturbed, red-stage and gray-stage classes (standard errors in Simard et al. 2011: Fig. 4). Low within-class variability should maximize the detection of among-class differences in surface fuels yet none were found

among the undisturbed, red-stage, and gray-stage classes.

Model adequacy

In our study, we used NEXUS, a modeling system that represents the current state of knowledge in fire behavior and that uses the same structure as other well-established and often-used models including Behave-Plus, FARSITE, and FFE-FVS (Scott and Reinhardt 2001, Scott 2006). These models have several recognized shortcomings, such as their systematic underestimation of potential crown fire behavior (Cruz and Alexander 2010). However, this weak point did not affect the results and conclusions of our study because our goal was not to predict the absolute, calibrated values of the fire behavior output variables but rather to determine the relative differences among time-since-beetle classes. As noted by Jolly et al., these models also do not represent the horizontal heterogeneity of fuels. However contrary to Jolly et al., we think that the explicit representation of canopy fuel heterogeneity would have further decreased the potential for crowning in the red and gray-stage stands because beetle infestations decrease the lateral continuity of canopy fuels. Increased spatial heterogeneity of fuels within tree crowns has been found to decrease the propagation of fire (Parsons et al. 2011) and this relationship probably holds at the scale of a canopy. In this regard, the model we used was probably conservative.

The shortcomings of these current models do represent incomplete understanding by the fire science field of the myriad of factors that affect fire behavior. And as often repeated, the statement that all models are wrong, but some models are useful is relevant here. Until more mechanistic models are developed and made widely available, the current models, albeit not ideal, will be used. The limited suite of modeling approaches from which to choose is also underscored by the fact that, although Moran and Cochrane and Jolly et al. both considered our modeling framework to be inadequate for studying beetle outbreak effects, they both used it to support their own perspective.

Conclusion

The concerns expressed by Moran and Cochrane (2012) and by Jolly et al. (2012) do not refute our finding that outbreaks of the MPB did not increase the predicted potential for active crown fires in lodgepole pine forests of Greater Yellowstone. We do not conclude that beetle-killed forests will not burn intensely under extreme fire weather conditions—they certainly will—only that the available evidence indicates that the potential for active crown fire in such stands is not necessarily greater than in a green forest under the same weather conditions. Our study purposefully did not address other aspects of fire behavior, such as spotting distance and soil heating, which may be affected by the outbreak.

Moran and Cochrane's and Jolly et al.'s comments are primarily based on three common misconceptions: that stand-level beetle-caused tree mortality is often extreme (i.e., >90% basal area killed), that stand-level tree mortality is synchronous, and that the entirety of needle biomass falling from beetle-killed trees is added to the forest floor litter in a completely cumulative pulse. Instead, we show that MPB infestations are a partial and slow disturbance, and that the decomposition of the slow input of pine needles explains the absence of a substantial increase in litter mass in red- and gray-stage stands. Consequently, Jolly et al.'s modeling results based on red-stage stands with 100% tree mortality and 100% dead needle retention are unrealistic and misleading. Similarly, modeling results based on red and gray-stage stands with inflated dead surface fuel loads are unfounded. We agree with Jolly et al. and Moran and Cochrane that canopy and surface fuel dynamics must be realistically evaluated in order to increase our understanding of pathogen-fire interactions; as such, it is essential that analyses are based on realistic field-based observations of beetle-outbreak dynamics (timing, severity) rather than simplified preconceptions about such dynamics.

Our modeling results are based on a robust empirical data set of surface and canopy fuels. The monitoring of individual beetle-killed trees would give invaluable data about the persistence and fall rates of red needles; until then, our fuel data are some of the best available. The change in fire behavior brought about by MPB infestation may ultimately only be resolved by experimental fire studies, which so far have been unable to detect an effect of simulated MPB outbreak on fire behavior (Schroeder and Mooney 2009).

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