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Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada

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Abstract:

After affecting millions of hectares of pine forests in western Canada, the mountain pine beetle (MPB; *Dendroctonous ponderosae* Hopkins) is spreading out of its native range and into Canada's boreal forest. Impacts of outbreaks can be environmental, economic, and social, and an ecosystem services (ES) viewpoint provides a useful perspective for an integrated approach to assessing these impacts and may help to identify how possible management strategies could minimize these impacts. In this regards, a comprehensive overview of the ecosystem functions and socioeconomic factors that have been impacted by the current outbreaks in western Canada was carried out to facilitate a more general ES assessment. In addition to timber production, current MPB outbreaks have negative effects on provisioning services (water supply and food production) and aesthetic cultural services, while effects on regulating services (carbon and forest fire) are still in debate. Among the supporting services, nutrient cycling and aquatic habitat showed short- and long-term negative effects, while terrestrial habitat showed a mostly positive response. The overall impact on ES may be more severe if salvage logging is practiced as a post-MPB forest management strategy. The outcomes of this study may help to identify areas of greatest socioecological vulnerability to MPB and identify knowledge gaps and avenues for research to advance the ES framework for MPB outbreak management.

Key words: ecosystem function, lodgepole pine, provisioning services, regulating services, salvage logging.

Résumé :

Après avoir dévasté des millions d'hectares de forêt de pin dans l'ouest du Canada, le dendroctone du pin ponderosa (DPP) se répand a` l'extérieur de son aire de répartition indigène dans la forêt boréale canadienne. Les impacts des épidémies peuvent être environnementaux, économiques et sociaux et l'angle des écoservices (ES) offre une perspective utile pour une approche intégrée de l'évaluation de ces impacts et peut aussi bien aider a` identifier comment des stratégies potentielles d'aménagement pourraient minimiser ces impacts. À cet égard, une synthèse complète des fonctions de l'écosystème et des facteurs socio-économiques qui ont subi l'impact des épidémies en cours dans l'ouest du Canada a été effectuée pour faciliter une évaluation plus générale des ES. En plus de la production de matière ligneuse, les épidémies actuelles du DPP ont des effets négatifs sur les services d'approvisionnement (alimentation en eau et production de nourriture) et les services esthétiques et culturels, tandis que les effets sur les services de régulation (carbone et feux de forêt) sont encore controversés. Parmi les services de support, le recyclage des nutriments et l'habitat aquatique ont subi des effets négatifs a` court et long terme tandis que l'habitat terrestre a surtout réagi positivement. L'impact global sur les ES pourrait être plus sévère si la coupe de récupération est utilisée comme stratégie d'aménagement forestier après le passage du DPP. Les résultats de cette étude peuvent aider a` identifier les zones de plus grande vulnérabilité socio-écologique au DPP ainsi qu'a` identifier les lacunes dans les connaissances et les avenues de recherche visant a` améliorer le cadre des ES pour la gestion des épidémies du DPP. [Traduit par la Rédaction]

Mots-clés*: fonction de l'écosystème, pin ponderosa, services d'approvisionnement, services de régulation, coupe de récupération.

1. Introduction

Outbreaks of mountain pine beetle (MPB; *Dendroctonous ponderosae* Hopkins) are natural phenomena that play a critical role in the development of western North American pine forests (Safranyik and Carroll 2006; Negrón and Fettig 2014). Beetles are part of a natural cycle that helps to maintain biologically diverse and functionally healthy forest landscapes (Axelson et al. 2009) by opening gaps in the forest canopy that permit understory regeneration and by creating habitat for avian and other species that use the standing deadwood. Patterns of MPB outbreaks appear to be changing with the changing climate and degree of human intervention (active forest management) in the forest (Taylor and Carroll 2004; Bentz et al. 2010). Forest management (e.g., harvest regulation, fire suppression) has increased the abundance of susceptible pines (*Pinus* spp.) in western Canadian forests, and warming climates (warmer summer, milder winter) are expanding the geographic range over which the beetle can complete its life cycle (Logan and Powell 2001; Carroll et al. 2006). As a result, over the past 15 years, the MPB population has expanded exponentially across its native range in lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) stands in British Columbia (BC) and moved east of the Rocky Mountains, spreading through boreal lodgepole and jack (*Pinus banksiana* Lamb.) pine stands in Alberta (McIntosh and Macdonald 2013; Erbilgin et al. 2014).

Generally, MPB burrow into the stems of susceptible pine trees, killing the host tree within a year of establishment. Female beetles lay their eggs along the sides of vertical galleries that they excavate in the inner bark of the mature tree. Once the eggs hatch, the beetle larvae feed on the phloem tissue of the tree and disrupt nutrient flow and eventually start damaging the host plant (Safranyik and Carroll 2006). MPB usually overwinter as larvae, completing their development the following spring, pupating in June or July, and finally the adults emerge in mid to late summer

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(Safranyik and Carroll 2006). Typically, MPB attacks larger diameter (diameter at breast height (DBH) >20 cm) (Amman et al. 1977) and older (>60 years) trees (Shore et al. 2006). However, the current MPB outbreak is more widespread and severe than in the past, and MPB has also been observed to colonize younger trees and stands (even 13 years of age and 7.5 cm DBH) in the absence of mature trees and stands (Maclauchlan 2006; Dhar et al. 2015). According to Shore et al. (2006), lodgepole pine mortality may approach 100% in mature stands growing in high climatic hazard areas, but landscape mortality level rates may more typically range from 25% to 50%. The current outbreak has impacted over 20 million hectares (Mha) of pine forests (18.5 Mha in BC and 1.54 Mha in Alberta) in western Canada, with partial to complete (stands with 100% pine) tree mortality since the current outbreak started in the late 1990s (Alberta Environment and Sustainable Resources Development (AESRD) 2012*a*; McIntosh and Macdonald 2013; Walton 2013). The eastward expansion of MPB outbreaks could extend to other native pine species across the boreal forest. However, this expansion is dependent on the availability of suitable climatic conditions (Bentz et al. 2010) and beetle population densities (McIntosh and Macdonald 2013). It has been predicted that boreal pine forests may lose 30% of their density or 40% to 60% of their standing volume if the intensity of attack is similar to what was observed in lodgepole pine forests in BC (Nealis and Peter 2008). Additionally, in the boreal region, lodgepole and jack pine often form even-aged, monospecific stands after fires, increasing the forest's susceptibility to a mass MPB outbreak. Standand landscape-level mortality and ES impacts due to MPB thus have the potential to be greater compared with other insect outbreaks for spruce or fir that are typically found in mixed boreal forests.

In BC and Alberta, wood from pine forests comprises 25% (Abbott et al. 2008) and 41% (based on coniferous harvest together with lodgepole and jack pine) (AESRD 2012*a*) of the province's timber supplies, respectively. The economic value of BC's wood products (all conifers

harvested) was \$9.07 billion (B) annually (all monetary values presented in this article are given in Canadian dollars unless stated otherwise) in 2010, with \$7.6 B (30% of BC's total export) annual timber export value (BC Ministry of Forests Mines and Lands 2010) and 64 800 direct jobs (7% of the total BC workforce). As of 2013, BC forest industries contributed \$2.5 B annually in revenues to the three levels of government (local, provincial, and federal) and 2.5% of provincial gross domestic product (GDP) (Meyers Norris Penny (MNP) 2015). In Alberta, provincial tax from the forest industry netted \$836 million (M) in stumpage, and forestry provides 13 000 jobs (AESRD 2012*a*; Alberta Government 2012). In addition to extensive timber losses, widespread MPB-caused tree mortality in pine forests may have significant implications for structural components of the ecosystem (e.g., vegetation, water, soil, etc.) (McCullough et al. 1998) and hence ecosystem services (ES). ES are the benefits that humans derive from nature (Millennium Ecosystem Assessment (MEA) 2005; The Economics of Ecosystems and Biodiversity (TEEB) 2010) and are generated from natural capital "stocks" from which ES flows like interest or dividends from those stocks (TEEB 2010). The concept of ES has emerged as a formal approach to describe and categorize the relationship between ecosystems and society and has become a prominent basis for planning and management in many regions worldwide (Daily 1997; Mooney and Ehrlich 1997). We propose that ES be considered in forest management decision making in support of adaptive management of existing areas impacted by MPB (i.e., in the provinces of BC and Alberta) and mitigation efforts in potentially susceptible areas (Saskatchewan and northeastern boreal forests). Doing so would provide a framework for assessing and minimizing the cumulative social, economic, and ecological consequences of outbreaks in western Canada.

In western Canada, the MPB-impacted forests are the sources of numerous essential ES (e.g., timber, fish, other forest products, fresh water, habitat for plants and animals, and recreational activities) that enhance quality of life and well-being for local people (Campbell et al. 2009) and

that benefit humans at larger scales. The current MPB outbreak has severely altered and affected many of these ES. Despite large numbers of studies about MPB impact on timber, post-MPB stand dynamics, carbon dynamics, hydrology, and wildlife (Abbott et al. 2008; Kurz et al. 2008; Bravi and Chapman 2009; Coates et al. 2009; Alfaro et al. 2010, Bunnell et al. 2011; Schnorbus 2011; Hawkins et al. 2012, 2013; Saab et al. 2014; Hansen et al. 2015; Hart et al. 2015; Dhar et al. 2015), researchers have rarely addressed the connections between MPB impact and ES. Moreover, an ES-based approach would provide a more comprehensive and holistic assessment than separate studies can do and would account for the myriad interconnections among impacts, ecological functions, and ES. We have, therefore, compiled this review to synthesize information that only relates to the consequences of MPB outbreaks on the overall forest ecosystem and the services that it provides. Our focus is pine forests in western Canada, which are experiencing the largest MPB outbreak in recorded history (Alfaro et al. 2010; Hawkins et al. 2012), and may significantly alter the ecosystem functions on local and regional scales. Therefore, the consequences of current MPB outbreaks become a significant challenge for forest managers, researchers, and practitioners of these areas. In addition, the area affected in western Canada is topographically diverse and includes boreal, montane, and dry interior forest types and thus may serve as an example for other regions. The main objectives of this review paper are threefold: (*i*) to review and synthesize information related to the impact of MPB outbreaks on ES; (*ii*) to describe the impact of MPB outbreaks on societal and ecosystem processes that affect ES; and (*iii*) to provide a brief outline of the consequences of current management policy on ES in MPB-impacted stands.

2. Ecosystem services impacted by MPB

Ecosystems provide a range of services that are of fundamental importance to human well-being, health, livelihoods, and survival (Costanza et al. 1997, 2014; MEA 2005; TEEB 2010), with

the concept of ES providing an operational understanding pursued in recent years by the UN Environment Programme under the Economics of Ecosystems and Biodiversity (TEEB) initiative (TEEB 2010). These ES can be categorized into four groups (MEA 2005): (*i*) provisioning services (i.e., timber, food, water, and other products obtained from ecosystems); (*ii*) regulating services (obtained from the regulation of the natural environment by ecosystem processes, i.e., fire, carbon storage, water quality); (*iii*) supporting services (necessary for maintenance of other services, i.e., habitat suitability or biodiversity, nutrient cycling); and (*iv*) cultural (nonmaterial benefits, e.g., recreation, aesthetic, spiritual). Our review follows the terminology and framework provided by these reports. Table 1 summarizes the list of ES examined and our main findings according to the subcategorization of provision, regulating, supporting, and cultural services as pertaining to potential changes in these ES with respect to MPB outbreaks.

2.1.   Impact on provisioning services

Provisioning services are perhaps the simplest to understand as these are the services that provide humans with tangible products (timber, water, food) (MEA 2005; TEEB 2010). They are also readily measured and valuated by conventional means. The current MPB outbreak has direct impacts on timber production, water supply, and nontimber forest product provisioning services.

2.1.1. *Raw materials*

2.1.1.1. *Timber production*

Timber provisioning has historically been a highly important ES (MEA 2005; TEEB 2010) that is directly linked to income generation and the economic viability of many communities and nations. In the province of BC, the current MPB outbreak has had a severe impact on this sector and has already killed a cumulative total of 723 million cubic metres (Mm^3) of pine (53% of the total merchantable pine volume) and infested 18.5 Mha of pine forests (Walton 2013); in Alberta,

approximately 25% of the pine forest has been infested and MPB continues to expand its ranges (AESRD 2012*b*). The initial response of forest managers to the outbreak was sanitation harvesting (Burton 2010) and insecticide (monosodium methanearsonate (MSMA)) application (Coops et al. 2008) to mitigate infestations; efforts eventually shifted to salvage logging operations (carried out almost exclusively by clearcutting) to capture as much economic value of the resource as possible in attacked pine stands before timber value deteriorated (Burton 2010). As a result, provincial governments have increased the annual allowable cut (AAC) by 14.5 Mm^3 in BC (Bogdanski et al. 2011) and 3.5 Mm^3 in Alberta (AESRD 2012*b*) from the pre-outbreak AAC levels to accommodate salvage logging activity. This additional supply of softwood timber is equivalent to an increase of 10.9% of Canadian and 4.0% of North American timber supply (based on year 2000 harvest levels; Bogdanski et al. 2011). However, the entire increased AAC in BC has never been met since 2007 due to the collapse of the US housing market (Bogdanski et al. 2011) and the subsequent decrease in demand for BC timber products. Although this increased amount of AAC has provided economic benefit for a short period of time, the AAC is expected to drop in most of the MPB-affected areas once salvage logging is over. In BC, AAC will drop approximately 12.6 Mm^3 below pre-outbreak levels, which will lead to a decrease of at least 20%, 7.5%, 4.5%, and 1.5% of the softwood timber supply of BC, Canada, North America, and the world, respectively (Abbott et al. 2008; Bogdanski et al. 2011). This will shrink BC's timber production potential to about $774 M annually (based on an AAC of 12.6 Mm^3 @ $61.41 \cdot m^{-3}$), including a possible decrease of $2.5 B in manufacturing activity, a loss of $250 M in government stumpage (the price charged by government to companies or operators for the right to harvest timber on public land) and royalty revenues, and a loss of 27 000 jobs (Abbott et al. 2008). In Alberta, MPB-caused tree mortality likewise has some level of impact on wood industries, as well as related service sectors, though detailed data are not available. Based on an assessment by Patriquin et al. (2007), BC's economy will not return to pre-MPB

business as usual (e.g., forest products contributing 30% of BC's total export and 20% of the provincial revenue) until forests are fully re-established — typically 60–80 years for regeneration to a mature forest stand in BC.

However, the scenario could be different than forecasted if salvage logging activity is carried out only where it is most beneficial (i.e., in forests that are not forecast to achieve minimum merchantable timber volumes (150 m$^3 \cdot$ha^{-1}) based on residual understory and surviving trees after the outbreak) (Burton 2006; Coates et al. 2006, 2009; Hawkins et al. 2012; Dhar et al. 2015). Multiple field investigations have revealed that a large percentage of MPBimpacted, unsalvaged stands have enough residual secondary structure (seedlings, saplings, subcanopy, and canopy trees that will survive a beetle attack) to provide minimum merchantable timber volumes (150 m$^3 \cdot$ha^{-1}) within 30 years (Coates et al. 2006, 2009; Pousette 2010; Hawkins et al. 2012; Dhar et al. 2013, 2015). Other studies have reported that only 17%–25% of unsalvaged stands may need some level of management intervention to achieve target merchantable midterm timber volumes (Coates et al. 2006; Dhar et al. 2013). In addition, surviving–residual understory and overstory tree species exhibited increased radial growth after outbreaks, although the extent of growth response varies considerably among species and sites (Axelson et al. 2009; Amoroso et al. 2013; Hawkins et al. 2013) and can be as high as 400% compared with the pre-MPB condition (Dhar et al. 2013). This implies that the recovery of timber production in most MPBimpacted, unsalvaged stands would be much faster than in the salvage-logged stands, and the money allocated for such management (plantations and land preparation expanses after salvage logging) activities can be utilized for other needed management activities such as rehabilitating those stands that require management intervention or to increase timber quality and volume.

2.1.2. Food

2.1.2.1.Other forest food products

Aside from timber harvest, a wide variety of products are collected from Canadian forests, including multiple species of mushrooms, berries, herbs, and animals hunted for food and fur, etc. (Duchesne and Wetzel 2002; Mitchell et al. 2006). All of these forest products are important from economic, social, cultural, and ecological viewpoints and contribute significantly to income and employment for forest-dependent communities (Duchesne and Wetzel 2002; Mitchell et al. 2006). Among these, commercial mushroom picking is one of the most important and documented income-generating products in western Canadian forests (Olivotto 1999; Bravi and Chapman 2009). The pine mushroom (*Tricholoma magnivelare*, or Canadian matsutake, which is an ectomycorrhizal species that exists in a symbiotic relationship with living pine trees and is not known to produce fruiting bodies without an associated tree host) is the most economically important species of wild mushrooms in western Canada and is severely affected by the current MPB outbreak (Bravi and Chapman 2009). It has been estimated that the economic value of pine mushrooms may exceed the value of timber production over a rotation period for a unit area (Olivotto 1999; Bravi and Chapman 2009). However, salvage logging after MPB attack has detrimental effects on pine mushroom habitat due to soil disturbance and reduced availability of living host trees (Bravi and Chapman 2009), leading to a longer recovery period compared with unsalvaged conditions in which pine mushroom habitat can be re-established within 15 years of infestation (Bravi and Chapman 2009).

In general, there is little understanding of how different forest foods and products (berries, herbs, or animals hunted for food and fur) have been impacted by the current MPB outbreak. However, numerous studies find a negative relationship between forest fruit production and canopy

closure. This relationship is most commonly discussed in relation to grizzly bear food sources in postfire stands and postharvest cut blocks (e.g., Nielsen et al. 2004) and is therefore not equivalent to human food collection and fruit picking in post-MPB stands. Nevertheless, it deserves highlighting that higher fruit production in disturbed stands can be explained by the positive relationship between fruit production and direct, incoming photosynthetically active radiation (Parks Canada 2001). Hamer (1996) found that forest canopy cover accounted for 70% of the variation in buffaloberry fruit production. Moola and Mallik (1998) found that reproductive performance of *Vaccinium myrtilloides* (blueberry) was greatest under partial shade conditions but recognize the site-specific conditions in that blueberry production is limited by shading from regenerating hardwoods and from mechanical damage to aboveground biomass associated with clearcutting. Finally, Larsen (2012) found that fruit production declines precipitously in cut blocks after about 20 years because of canopy closure, and Stone and Wolfe (1996) reported that frequency of fruit occurrence is positively related to increasing tree mortality but is highly variable. The response of food-provisioning ES is therefore mixed, and further detailed studies are recommended to ascertain the degree of impact on this ES sector.

2.1.3. Water provisioning

Forests in western Canada play a vital role in the terrestrial hydrological cycle by contributing to water provisioning (water yield), regulation (the seasonal distribution of flows), purification (quality), and aquatic habit ES; the latter two are discussed in the next section on regulating and supporting services. The current MPB outbreak combined with large-scale salvage logging has complex interactions among the different hydrological processes (i.e., evapotranspiration, local meteorology, snow accumulation, ablation, etc.) resulting in (*i*) increased snow accumulation and earlier and more rapid spring melt (Boon 2007; Embrey et al. 2012), (*ii*)

decreased evapotranspiration (Hélie et al. 2005; Embrey et al. 2012), (*iii*) decreased channel roughness due to removal of large woody debris leading to decreased flow attenuation (Bunnell et al. 2011), and (*iv*) extension of the channel network by roads, thereby increasing the drainage network and water delivery routes (Bunnell et al. 2011). Thus, MPB-caused tree mortality and logging activities have potential effects on water yield during the spring and early summer, as well as in the late summer (Wong 2008), which may increase the possibility of early season freshet, drier soils in the late summer, and water shortages at higher elevations and in late summer. Using a paired-watershed analysis in a 30% clearcut (salvage logged) of the total MPB-infested area in southern BC, Cheng (1989) found that annual water yields and peak flows increased by 21% with a 13-day advancement of peak flows in the spring. Similar results have also been reported in Montana (15% and 14–21 days) (Potts 1984). Other studies (Stednick 2007; BC Forest Practices Board 2007; Schnorbus 2011) have shown that MPB-caused mortality has a smaller impact on peak water flow compared with the cumulative effect of MPB and salvage logging. Post-MPB forest management by salvage logging may thus require extra caution, particularly in community watersheds, to minimize the impact on watershed ecosystem functions.

2.2. Impact on regulating services

Regulating services maintain essential ecosystem processes for human well-being and control rates of other services for stabilizing the supply of ES (MEA 2005; TEEB 2010). Disruption of any regulating service may threaten the sustainability of other essential ES. MPB-caused mortality has direct and indirect negative impacts on certain regulating services.

2.2.1. *Sediments and water purification: regulating services affecting water quality*

Changing water quality affects many aspects of human wellbeing, and benefits or costs accrue to different groups of beneficiaries at varying spatial and temporal scales. Water quality is,

therefore, an important regulatory ES that also contributes to other services including recreation and human health (MEA 2005; TEEB 2010). Forest ecosystems with intact ground cover and root systems are very effective at regulating water flow and improving water quality. The current MPB outbreak has changed forest structure, including the water and energy cycles that may potentially alter solute transport and, hence, water quality (Mikkelson et al. 2013). The overall impact on water quality is most likely greatest in areas that have been salvaged (Larkin et al. 1998; Wong 2008; Brown and Schreier 2009). Several studies reported that road density and the frequency of stream crossings increase during salvage logging, which, combined with potentially higher flows, leads to increased erosion and degradation of water quality by adding sediment, carbon, free radicals (NO_3), and minerals to water (Larkin et al. 1998; Mann et al. 2007; Stednick 2007; Wong 2008; Brown and Schreier 2009; Clow et al. 2011; Mikkelson et al. 2013). Based on expert opinion, sediments provide surfaces for microorganisms such as *Escherichia coli* (Migula.) and *Giardia* spp. to breed, which increases the risk of people suffering from waterborne illnesses (Wong 2008), as well as increasing the water turbidity, leading to increased gastrointestinal illness (Mann et al. 2007). Similarly, changes in organic carbon loading in the source water are very harmful for humans due to the production of carcinogenic disinfection by-products (DBP) during water purification with chlorine (Mikkelson et al. 2013). Based on a study in Colorado, an average of 300% more organic carbon and DBP was observed at water treatment facilities located in MPB-infested watersheds without salvage logging (Mikkelson et al. 2012). Considering other minerals, Brown and Schreier (2009) observed that ionic concentrations of total aluminum (Al) and other trace minerals showed significant increases during peak flow and decreases in low flow, while an opposite trend was observed for calcium (Ca), magnesium (Mg), and other soluble mineral or salt concentrations. These changes can necessitate increased water purification before human consumption.

2.2.2. *Extreme events: forest fire regulation*

The current MPB outbreak may also influence regulating services including forest fires, thus impacting human society in different ways (Mikkelson et al. 2012). In addition to timber loss, forest fires release particulates, carbon monoxide, carbon dioxide, and nitrogen oxides to the atmosphere, leading to decreased air quality that is directly linked to human health hazards and the economy (Mikkelson et al. 2012). In western Canada, forest fires and MPB outbreaks have increased in extent and severity during recent decades (Perrakis et al. 2014), thus raising concerns about their possible interactions (Negroìn et al. 2008). Generally, it is hypothesized that MPB-induced tree mortality affects fire behavior by altering the flammability, continuity, and structure of fuels (Lynch et al. 2006; Jenkins et al. 2008, 2014; Hicke et al. 2012*a*). Moreover, the profiles of surface, ladder, and crown fuels are expected to change with time since outbreak, potentially altering fire behavior and fire risk (Jolly et al. 2012; Jenkins et al. 2014). After tree death, needles fade to red within 1 year after MPB attack (red stage), and risks of ignition, torching, and canopy fire are expected to increase in this initial stage after MPB attack due to lower leaf moisture content (10 times lower in foliar moisture content compared with green needles) and greater percentage content of nonfibre carbohydrates and fats, which increase flammability (Jolly et al. 2012; Page et al. 2012). Some studies indicated that during the red stage, a high probability of active crown fire may occur (Page and Jenkins 2007; Hoffman 2011), while others predicted that passive fire (surface fire with torching of individual crowns), rather than active crown fire through the canopy, was more probable during this red stage (Simard et al. 2011; Klutsch et al. 2011). Approximately 3 to 10 years (gray stage) after the beetle attack, trees drop their needles and twigs and become exposed in the upper crown (Hicke et al. 2012*a*), which likely increases the forest floor fuels (Hicke et al. 2012*a*; Jenkins et al. 2014). Therefore, it is expected that surface fire will be more likely to spread into the canopy during the gray stage (Collins et al. 2012). However, empirical studies have

revealed mixed results; some studies report that MPB impact increases forest fire frequency and intensity (Lotan et al. 1985; Romme et al. 1986; Lynch et al. 2006; Jenkins et al. 2014; Perrakis et al. 2014), while others found no evidence of any relationship (Klutsch et al. 2011; Schoennagel et al. 2012; Bourbonnais et al. 2014; Harvey et al. 2014; Hart et al. 2015; Meigs et al. 2015) or concluded that there is a reduction in the probability of active crown fire in the short term by thinning lodgepole pine canopies (Alfaro et al. 2010; Simard et al. 2011). Other studies emphasize that climate has more effect than MPB outbreaks on the fire regime, with fire dynamics being driven primarily by weather conditions (i.e., extremely dry and gusty with a sustainable ignition event) and topography (Kulakowski and Jarvis 2011; Klutsch et al. 2011; Schoennagel et al. 2012; Harvey et al. 2014). These contrasting results suggest that MPB and its impacts on fuel accumulation and subsequent fire hazard are likely site-specific, change over time after infestation, and are interrelated with a number of other important environmental variables. Thus, the ongoing debate about how important outbreaks actually are to fire risk, relative to the potentially overriding influence of climate and weather on the fire regime, still persists.

2.2.3. *Climate regulation: carbon storage*

Carbon sequestration is an important regulating ES related to greenhouse gas (GHG) regulation (MEA 2005; TEEB 2010; Lal et al. 2013). The current MPB outbreak is expected to have a direct influence on carbon dynamics because tree mortality may reduce the rate of forest carbon uptake and increase future emissions through decomposition of dead trees (Kurz et al. 2008; Caldwell 2012; Hicke et al. 2012*b*). However, the net impact on carbon cycling is in debate, as different research approaches and studies have yielded different results (Foley et al. 2005; Kurz et al. 2008; Brown et al. 2010; Mathys et al. 2013; Emmel et al. 2014; Hansen et al. 2015). Based on modelled projections, Kurz et al. (2008) reported that the cumulative impact of the MPB outbreak

during 2000–2020 will be 270 megatonnes (Mt) of carbon or 990 Mt of carbon dioxide equivalent (CO_2e) GHG, which is comparable to 6 years of emissions (166 Mt CO_2e in 2010) from Canada's transportation sector or 10 years of emissions from the electrical sector (99 Mt CO_2e in 2010) (Environment Canada 2012). The total expected monetary value of GHG would be equivalent to $30.94 B (US dollar conversion in October 2015 @ 1.25 CA$) by 2020 based on the current price of carbon set by the International Monetary Fund (US$25 per tonne) (Litterman 2013). This suggests that vast tracts of forests are converting from a net C sink to a net C source, which affects carbon dynamics and will exacerbate global climate change (Foley et al. 2005). However, in contrast to this modelling projection, in a recent study, Arora et al. (2016) reported that the current MPB outbreak results in BC's forests accumulating 328 Mt less carbon over the period of 1999–2020, while changing climate and increasing atmospheric CO_2 concentration yield an enhanced carbon uptake equal to a cumulative sink of around 900–1060 Mt C, which is almost three times higher than the total loss during this same period. Similarly, field measurements from eddy flux towers in MPB-impacted stands suggest that forests are not changing from a net C sink to a net C source, because CO_2 uptake and water use efficiency (ratio of ecosystem C gain to evapotranspiration) did not change during the MPB outbreak compared with undisturbed forests (Reed et al. 2014). Other flux tower studies also reported that retaining healthy residual stems in the MPBimpacted forest results in higher C sequestration due to the rapidly regenerating undergrowth (growing-season C sink) compared with clearcut stands (C source) (Brown et al. 2010; Mathys et al. 2013; Emmel et al. 2014). A comparable result was also reported in a growth and yield modelling study by Hansen et al. (2015) for the central US Rockies. Likewise, other field-based growth dynamics studies in BC also conclude that in post-MPB conditions, the residual overstory and understory show increased radial growth compared with pre-MPB conditions (Coates et al. 2009; Amoroso et al. 2013; Hawkins et al. 2013; Dhar et al. 2013). This indicates a higher

carbon uptake by the residual tree species in post-MPB stands (Hansen 2014). Therefore, it is likely that MPB impacts on forest carbon are lower than originally predicted, and in some cases, MPB-caused mortality can stimulate stand growth and productivity (Kimmins 1987). However, this underscores the importance of maintaining healthy residual forest overstories and understories in MPB-affected areas and suggests that some management actions can be taken to sustain residual forest health as healthy forests can accumulate and sequester large amounts of carbon from the atmosphere (Fettig et al. 2013*a*).

2.3.   Impact on supporting services

Supporting services are those that are needed for the production of all other ES (MEA 2005). These kinds of services (i.e., habitat suitability, nutrient cycling) differ from other categories of ES as their impacts on society are either indirect or occur over a very long time (MEA 2005)).

2.3.1. *Habitat suitability or biodiversity*

2.3.1.1. Terrestrial habitat

In most cases, MPB outbreak emulates a thinning from above, which allows more growing space (light, water, nutrients, etc.) for surviving residual individuals and promotes growth (Dhar and Hawkins 2011). The current MPB outbreak has thus resulted in increased species richness and diversity for understory and herbaceous flora and fauna, although responses are highly variable (Kovacic et al. 1985; Stone and Wolfe 1996; Amoroso et al. 2013; Pec et al. 2015; Edwards et al. 2015; Perovich and Sibold 2016). Based on a recent study in western Alberta, Pec et al. (2015) reported that understory community diversity and productivity increased with the increase of tree mortality. Similar observations were also reported in lodgepole pine stands in northern Utah (Stone and Wolfe 1996) and in ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) stands in eastern Colorado (Kovacic et al. 1985). According to Kovacic et al. (1985), understory biomass increased

by 50% five years following beetle attack in ponderosa pine stands. In another study, Perovich and Sibold (2016) reported that MPB outbreak initiated a shift in forest structure from single-cohort lodgepole pine stands to stands with greater diversity in age classes and species composition. Conversely, MPB-caused mortality may have a negative impact on certain bryophytes and lichens as they require a more shaded habitat (Cichowski and Haeussler 2013), whereas light-loving ground lichens (*Cladina* spp., *Cladonia* spp., *Cetraria* spp.) may experience less impact. However, further studies regarding the response in bryophytes and lichens are required to fill this knowledge gap. Nonetheless, the majority of studies conclude that the occurrence of MPB attacks in most of the pinedominated stands results in more structurally and compositionally diverse stands, leading to multiple successional pathways different from those developed after logging or fire (Axelson et al. 2009; Dhar and Hawkins 2011; Hawkins et al. 2012; Amoroso et al. 2013; Dhar et al. 2015). Considering the species composition, MPBattacked forests are undergoing substantial conversion moving from lodgepole pine to more shade-tolerant species such as subalpine fir (*Abies lasiocarpa* Hook. Nutt.), white spruce, and their hybrid (*Picea glauca* Moench Voss × *Picea engelmannii* Parry) followed by low-to-moderate shade-tolerant species such as lodgepole pine and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Axelson et al. 2009; Dhar and Hawkins 2011; Hawkins et al. 2012; Amoroso et al. 2013; Perovich and Sibold 2016).

For wildlife species, MPB outbreaks may have direct (altering food availability), indirect (altering habitat suitability), or mixed impacts (Chan-McLeod 2006; Martin et al. 2006; Saab et al. 2014). Without salvage logging, MPB-caused mortality potentially benefits about 65% of the resident terrestrial vertebrate fauna, while salvage logging is anticipated to have negative effects on at least 35% of a total of 182 (127 birds, 50 mammals, four amphibians, and one reptile based on three major MPB-impacted forest districts) species inventoried in the ecosystem (Bunnell et al. 2004). The cavity-nesting species (e.g., black-backed woodpecker (*Picoides arcticus* S.))

responded more favorably to beetle-impacted forests than species with open-cup nests, as dead pine trees provide both food and nesting sites (Bonnot et al. 2008; Saab et al. 2014). Wildlife species that depend on the forest cover, however, showed negative responses (Bonnot et al. 2008). Mammalian species such as red squirrels (*Tamiasciurus hudsonicus* Erxleben) showed both negative (Drever and Martin 2007; Steventon 2015) and neutral (e.g., when non-host-tree species are present) responses (Saab et al. 2014), while a negative response was found for small mammals in salvage-logged stands (Sullivan et al. 2010). However, when the stand opens up due to snags falling down, significant beneficial effects accrue to wildlife as the forest structure changes to multilayered canopies with diverse classes and sizes of tree species (Chan-McLeod 2006; Saab et al. 2014). The MPB impact on species at risk such as woodland caribou (*Rangifer tarandus caribou* Gmelin) may be minimal because, despite the decrease in terrestrial lichen (species that woodland caribou prefer to eat) abundance and potential changes in snow conditions due to needle loss in pine forests, caribou still continue to crater for terrestrial lichens in matured killed pine stands (Cichowski 2010; Seip and Jones 2010). However, further study is required to validate MPB impact on caribou populations and their habitats. Although we have some level of understanding about the response of wildlife to MPB outbreaks, a significant knowledge gap still persists; therefore, detailed and long-term studies across different geographic locations are needed with emphasis on how different endangered species or species at risk respond to MPB outbreak.

2.3.1.2. Aquatic habitat

Commercial and sport fishing play an important role in Canada's national and regional economies and are highly dependent on freshwater habitats that serve as spawning and rearing grounds for many species of fish, including salmon (Zwickel 2012; Bailey and Sumaila 2013). The approximate cumulative value of current freshwater commercial fish production (BC: $445.4 M;

Alberta: $10 M) and sport fishing (BC: $957 M; Alberta: $488.1 M) is around $ 2 B annually (Alberta Agriculture, Food and Rural Development 2006; Statistics Canada 2012; Zwickel 2012; Bailey and Sumaila 2013). Based on a study in central BC, a total of 29 freshwater fish species are found, and one-quarter of these (e.g., bull trout (*Salvelinus confluentus* (Suckley, 1859)), salmon (*Oncorhynchus* spp., etc.)) are potentially (negatively) impacted by the combined effects of MPB and salvage logging; among these species, salmon would be the most severely impacted (Johannes et al. 2007). From the different studies, it is evident that MPB outbreaks in combination with large-scale salvage logging severely affect the forest watershed and its related aquatic environment (Bunnell et al. 2004, 2011); alteration of the aquatic environment by increased water flow, sedimentation, and temperature has direct negative effects on fish life cycles and, subsequently, fish production (Larkin et al. 1998; Wong 2008). Higher sedimentation could be lethal for resident and migratory fish populations present in the streams (Wong 2008; Bunnell et al. 2011). Although an MPB outbreak has minimal impact on water temperature (as grey-attack stands had higher shade values than harvested sites; see Forest Practices Board 2007; Rex et al. 2009), salvage logging from riparian areas after MPB attack could increase average water temperature by up to 1.5 °C in larger streams (river or canal) (Maloney 2004) and up to a maximum of 16 °C, with an average of 10 °C in small and shallow streams (Bunnell et al. 2004). As well, these temperature changes can persist over long periods, up to 10– 15 years (Johnson and Jones 2000). Increases in water temperature can cause growth inhibition, reduced survivability, increased susceptibility to disease, and alteration of fish egg and juvenile development (Ferrari et al. 2007; Johannes et al. 2007; Wong 2008). The physiology of migratory fish such as salmon and their egg development are directly impacted by higher water temperatures. Adult salmon cease feeding when they begin their migration from marine to fresh water and rely on their stored-up energy to return to their spawning

grounds (Rand et al. 2006), but in high water temperatures, their metabolic rate is accelerated, which causes early death (before spawning) (Ferrari et al. 2007).

Large woody debris (LWD) in streams is also critical for habitat formation; after a MPB attack, more LWD is imported into stream channels if no salvage logging operation is carried out. According to Hassan et al. (2008), in cases of 100% pine mortality, input rates of LWD in the stream may increase up to 3.7 times over rates before outbreak, ranging from 2.45 to 47.1×10^{-5} $m^3 \cdot m^{-2}$ annually. This may lead to development of relatively frequent and impermeable log jams, where riffles that serve as spawning areas (especially for salmon and trout (*Salmo* spp.)) are either buried or eroded, rearing pools are filled, and egg incubation environments are smothered with fine-textured sediments (Bisson et al. 1987). Any detrimental effects on salmon may have severe implications for the commercial fishing industry and fish-dependent communities, especially First Nations groups, as salmon has been a significant part of their culture and economy for thousands of years. On the other hand, LWD could provide breaks in the water current that serve as foraging sites for fish feeding on drifting food items and also form eddies where food organisms are concentrated. LWD also provides cover for bull trout as they require cool water for their physiological development (Hinch and Mellina 2008). However, further studies on responses of different fish species to MPB outbreaks may be required for better documentation. In addition to documented cascading impacts of MPB and subsequent salvage logging operations on fish habitats, this study also suggests that forest management by salvage logging should be restricted in riparian zones and limited in other areas of watersheds containing both fish-bearing and non-fish-bearing streams and lakes.

2.3.2. *Nutrient cycling*

Nutrient cycling is a key ES that contributes to supporting life on earth (MEA 2005). Generally, mineral nutrients from the soil are absorbed by trees as they grow, accumulate in their bodies, and are released when they die (Xue and Tisdell 2001). High tree mortality due to MPB attack can alter the nutrient cycling (nitrogen, phosphorus, organic carbon, metals, and base cations) processes in the soil (Mikkelson et al. 2013; Trahan et al. 2015). As trees begin to die following a beetle attack, nitrogen (N) uptake slows down and eventually ceases, which can lead to excessive nitrogen pools (increases in the rates of net N mineralization and nitrification) in the underlying soil until vegetation regrowth compensates (Griffin et al. 2011; Mikkelson et al. 2013; Cigan et al. 2015). Moreover, increased litter from the dead trees (Clow et al. 2011; Griffin et al. 2011; Cigan et al. 2015) can also increase inorganic nitrogen pools in the soil (Cullings et al. 2003). Transformation processes such as nitrification–denitrification and mineralization could be enhanced due to an abrupt increase in carbon sources, soil moisture, and microbial activity from higher energy fluxes in the ground (Mikkelson et al. 2013). However, confounding factors such as catchment nitrogen deposition, surviving vegetation, and climate can lead to different responses after MPB infestation (Mikkelson et al. 2013). Phosphorus (P) flux, in the form of either dissolved phosphate or particulate P, has the potential to be altered after a MPB attack as phosphate is readily released from decaying organic matter (Mikkelson et al. 2013). The MPB outbreak could also influence dissolved organic carbon (DOC) concentrations as decreases in canopy cover can increase runoff rates, and excess needle loss onto the forest floor compounded by soil moisture and temperature leads to increased decomposition and soil organic matter leaching (Mikkelson et al. 2013; Trahan et al. 2015). According to Trahan et al. (2015), DOC, dissolved organic nitrogen (DON), and inorganic phosphorus (PO_4^{3-}) concentrations in the soil decline up to 45%–51%, 31%–42%, and 53%–55%, respectively, within 4 years after MPB attack, but in 5–6 years after an attack,

DOC, DON, and PO_4^{3-} recovered to 71%–140% of those levels measured in undisturbed plots. In another study, Clow et al. (2011) observed no significant changes in stream-water NO_3 or DOC; however, total N and P increased. Interestingly, Griffin et al. (2011) and Keville et al. (2013) concluded that although MPB outbreaks significantly altered the N cycling, the net effects were surprisingly minor given the extent of the beetle-caused mortality. Conversely, MPB outbreaks may also influence cation and aluminum fluxes as increased nitrification reduces the soil pH and leads to the exchange and loss of base cations (Ca^{2+}, K^+, Mg^{2+}); however, further studies are required to confirm these changes. Based on the above discussion, it can be suggested that MPB outbreaks may have short-term impacts on nutrient cycling, but long-term monitoring may be required to determine whether biogeochemical changes are indeed more subtle in MPB-impacted pine ecosystems.

2.4. Impact on cultural services

Cultural ES are more difficult to define and measure as they are tightly bound to human values, behaviour, and socioeconomic conditions, which may differ widely across groups of people and even among individuals (MEA 2005; TEEB 2010). Cultural ES are most commonly defined as those services that enhance emotional, physical, and cognitive well-being for people (Faber et al. 2006). In this section, the impact of the MPB outbreak on cultural services is presented in light of tourism, recreation, and aesthetic (visual or scenic beauty) services.

2.4.1. Tourism and recreation

Tourism and recreation is an ES defined as the "recreational pleasure people derive from natural or cultivated ecosystems" (MEA 2005; TEEB 2010). This service is a very important revenuegenerating ES sector that is rapidly expanding with the increase of human mobilization, and it plays a significant role in western Canada's economy. The average estimated direct earnings

by the government from recreational sites was \$35.3 M (\$17.7 M in BC and 17.6 M in Alberta) in 2012 (BC Ministry of Environment 2013; Alberta Tourism, Parks and Recreation 2014). Other than direct revenue, users of forests and recreational sites are also contributing to different regional and socioeconomic sectors (i.e., job creation, local business, etc.). This service sector contributed approximately \$392 M and over 5200 full-time jobs in 2012–2013 in BC (BC Ministry of Environment 2013). In addition to having direct economic benefits to the province, users of recreational sites benefit in nontangible ways through stress reduction, increased physical fitness, and overall well-being, thus leading to reductions of \$4.4 M to \$6.7 M in healthcare costs annually (BC Ministry of Forests, Lands and Natural Resource Operations 2012).

There are 2275 recreational sites or provincial parks in BC and Alberta (1319 in BC and 1258 in Alberta) and 1151 designated recreational trails (818 in BC and 333 in Alberta) with an average of 20.8 M visitors each year. The current MPB outbreak has affected almost 80% of recreational sites and trails in the central BC Interior (BC Ministry of Forests, Lands and Natural Resource Operations 2012), while in Alberta, the effect is not as severe. However, with one exception (Kootenay National Park), no park campgrounds or trails were closed in BC after the outbreak (Tory Stevens, Ecologist, BC Parks, personal communication). It appears that the MPB outbreak has neither extensively nor negatively impacted local recreational activity in impacted areas in BC (Meitner et al. 2011), and at the same time, visitor use expanded by 5.5%–7.5% during the outbreak period (BC Ministry of Environment 2008, 2013). Conversely, negative impressions expressed by recreational users were reported in MPB-infested Banff National Park and Kootenay National Park (McFarlane et al. 2006; McFarlane and Watson 2008) in Canada. In another study, Rosenberger et al. (2013) mentioned that MPB outbreaks result in significant losses in recreation values, at least in the short term, while moderate to severe MPB outbreaks can cause losses in total recreation values from \$5 M to \$59 M and may reduce recreation visitation by 0.5 M user days at

maximum outbreak levels in Rocky Mountain National Park, USA (Rosenberger et al. 2013). However, when we look at the overall visitation and revenue of Kootenay National Park in Canada from 2005–2010 (daily entrance and camping attendance), there was an increase from 1.34 to 1.42 M tourists and $1.33 to $1.77 M during the peak MPB attack season, respectively (BC Ministry of Environment 2010). This implies that although tourists' attitude toward beetle impact may have been negative (McFarlane et al. 2006; McFarlane and Watson 2008), overall visitation and revenue earnings were not affected by MPB in Canadian national parks. The overall impact of MPB outbreak on tourism and recreation revenue and visitor numbers, as well as on the visitor experience, thus seems to have been minimal.

2.4.2. *Aesthetic–visual–scenic beauty*

Aesthetic value is an ES that relates to people's appreciation of natural scenery in ways other than through deliberate recreational activities (TEEB 2010). Aesthetic appreciation of forest land and urban, rural, or coastal landscapes is one of the most fundamental ways in which people may experience and relate to their physical environment. Sometimes called visual quality, scenic beauty of the environment is a well-recognized and accepted dimension of aesthetic appreciation. Insect outbreaks produce a wide range of visual effects depending on the forest type, the specific insect, geographic location, and many other factors, including temporal stage and biophysical condition (Rosenberger and Smith 1998; Sheppard and Picard 2006). Generally, after a MPB attack, the colour of the trees goes through three stages: (*i*) the green stage, in the first year after an attack; (*ii*) the red stage, up to 4 years after an attack when foliage turns brownish and then red; and (*iii*) the grey stage, more than 4 years after an attack when the dead tree has lost its needles. The remaining gray boles provide the predominant visual effect until forest regeneration and recovery occurs, which can often take 20–30 years. Most studies clearly document that MPB-caused

mortality negatively affects the visual quality of the forests (Buhyoff et al. 1982; Daniel et al. 1991; Rosenberger and Smith 1998; Sheppard and Picard 2006; BC Ministry of Forests and Range 2010; Meitner et al. 2011) and consequences could be more dramatic at high levels of attack (Daniel et al. 1991; Sheppard and Picard 2006). Based on a survey in six MPB-impacted communities in BC, Meitner et al. (2011) reported that most of the respondents were deeply concerned about the visual impact on the forest, although their recreational activity during the infestation was more or less the same as before. Although MPB outbreak has significant impact on the scenic beauty, public perceptions appear to be complex and poorly understood.

3. Management of MPB outbreaks

In western Canada, MPB management was first initiated when lodgepole pine timber value grew in the early 20th century. The initial response was to destroy the beetle through direct control (cruising, decking, and burning) (Hopping and Mathers 1945). However, with the advancement of scientific knowledge, the emphasis increasingly shifted away from direct pest management to a holistic forest management approach to reduce detrimental effects (Safranyik et al. 1974). Since then, research has increasingly focused on developing decision support tools such as hazard- and risk-rating systems for stands susceptible to beetle attacks (Amman et al. 1977; Amman and Anhold 1989; Shore and Safranyik 1992, 2004). Attention has thus gradually shifted from reactive (direct control) to proactive (preventive) MPB management. Over the past two decades, considerable research effort has focused on development of landscape-level models (Riel et al. 2004) to predict patterns of MPB outbreak development, comparing potential outcomes of control strategies and project impacts on forest management objectives (Fall et al. 2004). In spite of significant advancement in MPB management, none of this knowledge can solely mitigate the problem, and management still depends on sanitation harvesting to control infestations by removing infested

trees, use of prescribed fire, insecticides (MSMA), semiochemicals, or pheromones used on trap trees (Coops et al. 2008; Fettig et al. 2014; Gillette et al. 2014). Unfortunately, the effectiveness of some of these direct management approaches (sanitation, insecticide, semiochemicals) do not last more than 2 years, some have a negative effect on the environment (insecticide), and some require higher cost, skills, and labour (sanitation, prescribed fire) to implement (Fettig et al. 2007, 2013*b*; Coops et al. 2008; Wulder et al. 2009; Gillette et al. 2014; Progar et al. 2014). On the other hand, some researchers suggest indirect management or preemptive logging in advance of beetle infestation such as thinning from below, tree crown thinning, and selection thinning treatments (Dahlsten and Rowney 1983; Mitchell et al. 1983; Fettig et al. 2007). Most of these indirect approaches may effectively control the beetle for 20–30 years at the initial stage of beetle spread; however, such approaches are more labour intensive and may require a huge financial investment to carry out at the field level and need to be applied before beetle outbreaks (Dahlsten and Rowney 1983; Mitchell et al. 1983; Fettig et al. 2007; Coops et al. 2008). In the context of western Canada, these approaches may be suitable at the beginning of a MPB infestation or a small-scale attack, but in cases of outbreak infestation, none of these approaches would be effective or suitable due to the large extent of pine forests (>25 M ha), the lack of manpower to implement, inaccessibility to many beetle-impacted areas, economic constraints, and the large spatial extent of the beetle population. Therefore, management of MPB outbreaks should be diverted to a post-MPB stand management strategy by (*a*) using salvage logging to reduce the economic impact (to recover the value of dead standing timber) of a beetle outbreak and (*b*) facilitate stand re-establishment where needed (Burton 2010; Dhar et al. 2015). While these management interventions are generally carried out within the constraints of government regulations that require some protection of wildlife habitat and riparian areas, their principal purpose is to protect and recover standing timber for commercial interests. Given the large spatial extent of MPB outbreaks, the potential landscape- and ecosystem-scale

impacts of timber-based management approaches to control and mitigate the effects of infestations are significant over decadal time scales. We argue that management of MPB-impacted forests should take a systems-level approach that considers the multiple interacting processes in a forest necessary for the maintenance of a wide range of supporting, provisioning, and regulating ES.

As this review has shown, large-scale salvage logging may have significant negative effects on multiple forest ES, including timber production, biodiversity, water quality and provisioning, aesthetic or scenic beauty, and aquatic habitats (Dhar and Parrott 2015). The clearcut logging practices widely used throughout the region (for salvage or preemptive harvesting in response to the MPB outbreak) create a homogenous, even-aged landscape structure that undermines many ES, has negative impacts on biological diversity, and may impair ecosystem recovery and resilience due, in part, to the maladaptation of some species to the interactive effects of two disturbance events (MPB and logging) (Lindenmayer et al. 2008; Burton 2010; Dhar and Hawkins 2011; Dhar and Parrott 2015; Dhar et al. 2015). Such homogenous, even-aged stands would be more susceptible to future natural disturbances such as MPB and fire. Conversely, if MPB-impacted stands were left untreated or unsalvaged, most of the stands in western Canada would convert into a heterogeneous landscape structure where mosaics of even-aged and uneven-aged patches are interspersed in space (Agee 1993; Burton 2010; Dhar and Hawkins 2011; Amoroso et al. 2013; Gillette et al. 2014; Dhar et al. 2015). The ES provisioning in these heterogeneous forests can recover faster from MPB impacts than the salvage logged stands, as a significant portion of biological legacies (i.e., surviving trees, snags and logs, patches of intact vegetation, and seedbanks in tree crown or in the soil) of that particular ecosystem remain intact (Gustafsson et al. 2012; Lindenmayer et al. 2012; Fedrowitz et al. 2014; Dhar et al. 2015). This allows the forest to "remember" its genetic, compositional, and structural preharvest condition, contributing to regeneration of a new complex ecosystem (Drever et al. 2006; Dhar et al. 2015). This ecosystem memory is likely an important factor necessary for

maintaining resilience of MPB-impacted stands. All evidence suggests that unsalvaged stands are more resilient than salvaged stands and can maintain the identity, structure, and function of an ecosystem after disturbance, as well as significantly reduce susceptibility to future MPB infestation (Drever et al. 2006; Lindenmayer et al. 2008; Schowalter 2012; Dhar and Parrott 2015; Dhar et al. 2015). In addition, accelerated timber harvesting has significant negative impacts on different ES by influencing the ecosystem processes and related biota. Thus, from a whole-system perspective in which maintenance of a range of ES is a management objective, salvage logging to accelerate short-term timber volumes may not always be the best post-MPB management response. Research suggests that the large number of residual green trees that have survived the beetle outbreak in MPB-affected forests may provide valuable midterm timber volumes, habitat, and ecosystem benefits when they are most needed after a beetle outbreak (Burton 2010; Six et al. 2014; Dhar et al. 2015). Our argument here is not to forego management, but rather that management should be led by science and monitoring where socioecological considerations, the best available data, local and expert knowledge, professional judgment, and long-term cost–benefit assessments (based on a range of ES beyond timber production) need to be considered.

4. Conclusions

The current MPB outbreak in western Canada affects different ES both positively and negatively. From a critical analysis of the current literature, the following generalization statements about the MPB-infested forests in western Canada can be made, although knowledge gaps persist.

- Provisioning services: Timber production is the most severely affected ES, followed by water supply and food (berries and pine mushroom). Impacts on these services may directly contribute to economic crises and social cohesion in forest dependent communities.

- Regulating services: Water quality is the most severely impacted regulating ES, while debate persists regarding the impact of MPB outbreaks on forest fire regulation and carbon dynamics or climate stabilization.

- Supporting services: Among supporting services, most of the components of terrestrial habitat services showed positive responses, whereas most of the components of aquatic habitat showed negative responses to MPB outbreaks. Nutrient cycling also showed a short-term negative effect.

- Cultural services: Tourism and recreation do not show any documented detrimental effects in response to the current MPB outbreak, while the outbreak has potential negative effects on services related to landscape aesthetics or scenic beauty. The effects of MPB infestations on public perceptions appear to be complex and much is not yet understood due to limited studies, therefore further investigations are recommended to explore the ramifications of the MPB outbreak and societal response to it.

All evidence suggests that MPB outbreaks in combination with salvage logging significantly increase impacts on most of the ES, whereas in the absence of salvage logging, MPB outbreaks have a comparatively lesser impact. Consequently, any management response to natural disturbances such as MPB need to carefully balance economic concern for recouping the lost timber value and preserving the nontimber benefits with the ecological realization that disturbance is an integral part of forest health and function.

5. Future direction of research

Based on this review, it is clearly evident that in spite of numerous studies, little is known about the long-term effect of MPB outbreaks on different ecosystem functions and society (such as habitat quantity and quality, hydrological integrity, forest fire dynamics, carbon cycling, endangered plant and wildlife species, and spiritual or aesthetic factors including the socioeconomic impact on forest-

dependent communities of affected regions) (Table 1). Therefore, future research should address the following points to increase our understanding of the causes and consequences.

- It is necessary to distil the essential climatic, ecosystem component, watershed, social, and beetle attack variables that impact different ecosystem services supply and demand to support predictive understanding and a model for future MPB management that works across the different scales of distance and time.

- In addition to detailed studies, mapping the influences of MPB outbreak on local, regional, and national scales will provide a basis to identify where and which part of the landscape has been most severely impacted by the MPB and requires attention from a mitigation program.

- Studies on societal response to MPB attacks could provide the basis to identify at-risk forest-dependent communities and their degree of vulnerability to MPB attack.

- To date, management responses have emphasized only shortterm exploitation of a single provisioning (timber) value rather than long-term stewardship of multiple ecosystem services and respect for all forest ES values. MPB and ecosystem management decisions, therefore, should be considered in terms of long-term trade-offs between the costs and benefits among ES. Although our understanding of the complex nature of ecosystems, the interrelationships between processes at the landscape scale, and the benefits that they provide to humans is still limited, a better understanding of the dynamics of multiple ES impacted by the current MPB outbreak may help to quantify the provisioning of multiple services, their trade-offs, and the synergies among them. Such an understanding would greatly contribute to the sustainable management of forested landscapes, in general, and to the management of human responses to ongoing and future forest disturbances.

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References

Abbott, B., Stennes, B., and van Kooten, G.C. 2008. An economic analysis of mountain pine beetle impacts in a global context. REPA working paper 2008-02, University of Victoria, B.C.

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Alberta Agriculture, Food and Rural Development. 2006. Fresh water aquaculture industry, agriculture business profiles. Alberta Ministry of Agriculture, Food & Rural Development. Available from http://www1.agric.gov.ab.ca/ $department/deptdocs.nsf/all/agdex4258#Economic [accessed 24 May 2015].

Alberta Environment and Sustainable Resources Development (AESRD). 2012*a*. Economic impact of Alberta's forest sector 2012. Alberta Government, Alberta. Available from https://www.albertacanada.com/AlbertaForestSector2012EconomicImpact.pdf [accessed 26 May 2015].

Alberta Environment and Sustainable Resources Development (AESRD). 2012*b*. Sustainable forest management: 2012 facts & statistics. Alberta Government, Alta. Available from https://open.alberta.ca/dataset/97143d64-3e65-40a09e04-a207b36feb38/resource/9577b519-a039-43cc-b55a-8c0c487e915a/ download/FMPs-2012.pdf [accessed 24 May 2015].

Alberta Government. 2012. Highlights of the Alberta economy 2012. Edmonton, Alberta. Available from http://www.albertacanada.com/SP-EH_highlights ABEconomy.pdf [accessed 22 May 2015].

Alberta Tourism, Parks and Recreation. 2014. Tourism, parks and recreation, Annual report 2013–2014. Alberta Government. Available from http://culture.alberta.ca/ about/annualreport/2014/TPR/AnnualReport-withstatements.pdf [accessed 22 May 2015].

Alfaro, R.I., Campbell, E., and Hawkes, B.C. 2010. Historical frequency, intensity and extent of mountain pine beetle disturbance in British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., MPB Working Paper 2009-30.

Amman, G.D., and Anhold, J.A. 1989. Preliminary evaluation of hazard and risk variables for mountain pine beetle infestations in lodgepole pine stands. *In* Proceedings of the Symposium on the Management of Lodgepole Pine to Minimize Losses to the Mountain Pine Beetle, Kalispell, Montana, 12–14 July 1988. *Edited by* G.D. Amman. USDA Forest Service, General Technical Report INT-262. pp. 22–27.

Amman, G.D., McGregor, M.D., Cahill, D.B., and Klein, W.H. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Service, General Technical Report INT-36.

Amoroso, M.M., Coates, K.D., and Astrup, R. 2013. Stand recovery and selforganization following large-scale mountain pine beetle induced canopy mortality in northern forests. For. Ecol. Manage. **310**: 300–311. doi:10.1016/j. foreco.2013.08.037.

Arora, V.K., Peng, Y., Kurz, W.A., Fyfe, J.C., Hawkins, B., and Werner, A.T. 2016. Potential near-future carbon uptake overcomes losses from a large insect outbreak in British Columbia, Canada. Geophys. Res. Lett. **43**: 2590–2598. doi:10.1002/2015GL067532.

Axelson, J., Alfaro, R., and Hawkes, B. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. For. Ecol. Manage. **257**: 1874–1882. doi:10.1016/j.foreco.2009.01.047.

Bailey, M., and Sumaila, U.R. 2013. Freshwater angling and the BC economy. Freshwater Fisheries Society of B.C., Victoria, Economic impact report.

BC Forest Practices Board. 2007. The effect of mountain pine beetle attack and salvage harvesting on streamflows. BC Forest Practices Board, Victoria, Special Investigation FPB/SIR/16.

BC Ministry of Environment. 2008. 2007/08 BC Parks year end report. Available from http://www.env.gov.bc.ca/bcparks/research/year_end_report/ year_end_rep_2008.pdf [accessed 14 June 2015].

BC Ministry of Environment. 2010. 2009/10 BC Parks year end report. Available from http://www.env.gov.bc.ca/bcparks/research/year_end_report/ year_end_rep_2010.pdf [accessed 14 April 2015].

BC Ministry of Environment. 2013. BC Parks 2012/13 statistics report. Available from http://www.env.gov.bc.ca/bcparks/research/statistic_report/ statistic_report_2013.pdf [accessed 22 June 2015].

BC Ministry of Forests, Lands and Natural Resource Operations. 2012. Resource values assessment: recreation, a mid-term timber supply action plan. Available from http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/mid-termtimber-supply-project/Recreation_summary_june11.pdf [accessed 11 April 2015].

BC Ministry of Forests, Mines and Lands. 2010. The state of British Columbia's forests. 3rd ed. BC Ministry of Forests, Mines and Lands, Victoria, B.C. Available from http://www.for.gov.bc.ca/hfp/sof/2010/SOF_2010_Web.pdf [accessed 14 March 2015].

BC Ministry of Forests and Range. 2010. Visual impact of mountain pine beetle attack and resulting salvage operations in British Columbia: a public perception study. BC Ministry of Forests and Range, Forest Practices Branch, Victoria, B.C.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., and Seybold, S.J. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience, **60**(8): 602–613. doi:10.1525/bio.2010.60.8.6.

Bisson, P.A., Bilby, R.E., Bryant, M.D., Dollof, C.A., Grette, G.B., House, R.A., Murphy, M.L., Koski, K.V., and Sedell, J.R. 1987. Large woody debris in forest streams in the Pacific Northwest: past, present, and future. *In* Stream management: forestry and fisheries interaction. *Edited by* E.O. Salo and T.W. Cundy. University of Washington, Seattle, Washington. pp. 143–190.

Bogdanski, B., Sun, L., Peter, B., and Stennes, B. 2011. Markets for forest products following a large disturbance: opportunities and challenges from the mountain pine beetle outbreak in western Canada. Canada Forest Services, Report BC-X-429.

Bonnot, T.W., Rumble, M.A., and Millspaugh, J.J. 2008. Nest success of blackbacked woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. Condor, **110**(3): 450–457. doi:10.1525/cond.2008. 8460.

Boon, S. 2007. Snow accumulation and ablation in a beetle-killed pine stand in northern Interior British Columbia. J. Ecosyst. Manage. **8**: 1–13.

Bourbonnais, M.L., Nelson, T.A., and Wulder, M.A. 2014. Geographic analysis of the impacts of mountain pine beetle infestation on forest fire ignition. Can. Geogr. **58**: 188–202. doi:10.1111/j.1541-0064.2013.12057.x.

Bravi, B., and Chapman, B.K. 2009. Managing for pine mushrooms through the mountain pine beetle epidemic in the west Chilcotin. BC Ministry of Forests and Range, Kamloops, B.C., Extension Note 09.

Brown, M., Black, T.A., Nesic, Z., Foord, V.N., Spittlehouse, D.L., Fredeen, A.L., Grant, N.J., Burton, P.J., and Trofymow, J.A. 2010. Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia. Agric. For. Meteorol. **150**: 254–264. doi:10.1016/j.agrformet.2009. 11.008.

Brown, S., and Schreier, H. 2009. Water quantity and quality related to rates of pine beetle infestation and salvage logging: a regional comparison. Water Quality Technical Report, MPB Project No. 7.31.

Buhyoff, G.J., Wellman, J.D., and Daniel, T.C. 1982. Predicting scenic quality of mountain pine beetle and western spruce budworm damaged forest vistas. For. Sci. **28**: 827–838.

Bunnell, F., Squires, K.A., and Houde, I. 2004. Evaluating effects of large-scale salvage logging for mountain pine beetle in terrestrial and aquatic vertebrates. Natural Resources Canada, Victoria, B.C.

Bunnell, F.L., Kremsater, L.L., and Houde, I. 2011. Mountain pine beetle: a synthesis of the ecological consequences of large-scale disturbances on sustainable forest management, with emphasis on biodiversity. Canadian Forest Service, Victoria, B.C.

Burton, H.P. 2010. Striving for sustainability and resilience in the face of unprecedented change: the case of the mountain pine beetle outbreak in British Columbia. Sustainability, **2**: 2403–2423. doi:10.3390/su2082403.

Burton, P.J. 2006. Restoration of forests attacked by mountain pine beetle: misnomer, misdirected, or must-do? J. Ecosyst. Manage. **7**(2): 1–10.

Caldwell, M.K. 2012. Impacts of mountain pine beetle (*Dendroctonus ponderosae*) and fire disturbances on forest ecosystem carbon dynamics and species composition. M.Sc. thesis, University of Colorado, Denver, Colorado.

Campbell, E.M., Saunders, S.C., Coates, K.D., Meidinger, D.V., MacKinnon, A., O'Neill, G.A., MacKillop, D.J., DeLong, S.C., and Morgan, D.G. 2009. Ecological resilience and complexity: a theoretical framework for understanding and managing British Columbia's forest ecosystems in a changing climate. B.C. Min. For. Range, For. Sci. Prog., Victoria, B.C., Tech. Rep. 055.

Carroll, A.L., Régnière, J., Logan, J.A., Taylor, S.W., Bentz, B., and Powell, J.A. 2006. Impacts of climate change on range expansion by the mountain pine beetle. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., MPB Working Paper 2006-14.

Chan-McLeod, A.C.A. 2006. A review and synthesis of the effects of unsalvaged mountain-pine-beetle-attacked stands on wildlife and implications for forest management. J. Ecosyst. Manage. **7**: 119–132.

Cheng, J.D. 1989. Streamflow changes after clear-cut logging of a pine beetleinfested watershed in southern British Columbia, Canada. Water Resour. Res. **25**: 449–456. doi:10.1029/WR025i003p00449.

Cichowski, D. 2010. Tweedsmuir–Entiako Caribou Project: effects of a mountain pine beetle epidemic on northern caribou habitat use — final report. Prepared for the Bulkley Valley Centre for Natural Resources Research and Management, Smithers, B.C.

Cichowski, D., and Haeussler, S. 2013. The response of caribou terrestrial forage lichens to mountain pine beetles and forest harvesting in the East Ootsa and Entiako areas. Annual report — year 11, Habitat Conservation Trust Foundation, Victoria, and Ministry of Forests, Lands and Natural Resource Operations, Smithers, B.C.

Cigan, P.W., Karst, J., Cahill, J.F., Jr., Sywenky, A.N., Pec, G.J., and Erbilgin, N. 2015. Influence of bark beetle outbreaks on nutrient cycling in native pine stands in western Canada. Plant Soil, **390**: 29–47. doi:10.1007/s11104-014-2378-0.

Clow, D.W., Rhoades, C., Briggs, J., Caldwell, M., and Lewis, W.M. 2011. Responses of soil and water chemistry to Mountain Pine Beetle induced tree mortality in Grand County, Colorado, U.S.A. Appl. Geochem. **26**: S174–S178. doi:10.1016/j. apgeochem.2011.03.096.

Coates, K.D., DeLong, C., Burton, P.J., and Sachs, D.L. 2006. Abundance of secondary structure in lodgeople pine stands affected by mountain pine beetle. Report of Chief Forester, Bulkley Valley Centre for Natural Resources Research and Management, Smithers, B.C., Canada.

Coates, K.D., Glover, T., and Henderson, B. 2009. Abundance of secondary structure in lodgepole pine stands affected by the mountain pine beetle in the Cariboo-Chilcotin. Canadian Forest Service, Pacific Forestry Centre, Mountain Pine Beetle Working Paper 2009-20, Victoria, BC, pp. 37.

Collins, B.J., Rhoades, C.C., Battaglia, M.A., and Hubbard, R.M. 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. For. Ecol. Manage. **284**: 260–268. doi:10.1016/j.foreco.2012.07.027.

Coops, N.C., Timko, J.A., Wulder, M.A., White, J.C., and Ortlepp, S.M. 2008. Investigating the effectiveness of Mountain Pine Beetle mitigation strategies. Int. J. Pest Manage. **54**(2): 151–165. doi:10.1080/09670870701805737.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., and van den Belt, M. 1997. The value of the world's ecosystem services and natural capital. Nature, **387**: 253–260. doi:10.1038/387253a0.

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderon, S.J., Kubiszewski, I., Farber, S., and Turner, R.K. 2014. Changes in the global value of ecosystem services. Glob. Environ. Change, **26**: 152–158. doi:10.1016/j. gloenvcha.2014.04.002.

Cullings, K.W., New, M.H., Makhija, S., and Parker, V.T. 2003. Effects of litter addition on ectomycorrhizal associates of a lodgepole pine (*Pinus contorta*) stand in Yellowstone National Park. Appl. Environ. Microbiol. **69**(7): 3772– 3776. doi:10.1128/AEM.69.7.3772-3776.2003.

Dahlsten, D.L., and Rowney, D.L. 1983. Insect pest management in forest ecosystems. Environ. Manage. **7**: 65–72. doi:10.1007/BF01867043.

Daily, G. 1997. What are ecosystem services? *In* Nature's services: societal dependence on natural ecosystems. *Edited by* G.C. Daily. Island Press, Washington, D.C.

Daniel, T.C., Orland, B., Hetherington, J., and Paschke, J.L. 1991. Public perception and attitudes regarding spruce bark beetle damage to forest resources on the Chugach National Forest, Alaska. Final report prepared for the US Forest Service, Forest Pest Management, Anchorage, Alaska.

Dhar, A., and Hawkins, C.D.B. 2011. Regeneration and growth following mountain pine beetle attack: a synthesis of knowledge. J. Ecosyst. Manage. **12**: 1–16.

Dhar, A., and Parrott, L. 2015. Salvage logging after mountain pine beetle outbreaks reduces the social-ecological resilience of forest landscapes. *In* Mountain pine beetle information exchange forum Edmonton, AB, 22–23 July 2015. *Edited by* K. McClain.

Dhar, A., Coates, K.D., Rogers, B., and Hardy, K. 2013. Impact of mountain pine beetle on mid-term timber supply in sub boreal spruce zone of British Columbia. *In* Proceedings of the 16th International Boreal Forest Research Association (IBFRA), Edmonton, AB, 7–10 October 2013. *Edited by* P.G. Comeau.

Dhar, A., Balliet, N.A., Runzer, K.D., and Hawkins, C.D.B. 2015. Impact of a mountain pine beetle outbreak on young lodgepole pine stands in central British Columbia. Forests, **6**: 3483–3500. doi:10.3390/f6103483.

Drever, M.C., and Martin, K. 2007. Spending time in the forest: responses of cavity-nesters to temporal changes in forest health and environmental conditions in interior British Columbia. *In* Temporal dimensions of landscape ecology: wildlife responses to variable resources. *Edited by* J.A. Bissonette and I. Storch. Springer, New York. pp. 236–251.

Drever, R.C., Peterson, G., Messier, C., Bergeron, Y., and Flannigan, M. 2006. Can forest management based on natural disturbances maintain ecological resilience? Can. J. For. Res. **36**: 2285–2299. doi:10.1139/x06-132.

Duchesne, L.C., and Wetzel, S. 2002. Managing timber and non-timber forest product resources in Canada's forests: needs for integration and research. For. Chron. **78**(6): 837–842. doi:10.5558/tfc78837-6.

Edwards, M., Krawchuk, M.M., and Burton, P.J. 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: understory and overstory response to mountain pine beetle and fire. For. Ecol. Manage. **335**:

163–175. doi:10.1016/j.foreco.2014.11.011.

Embrey, S., Remais, J.V., and Hess, J. 2012. Climate change and ecosystem disruption: the health impacts of the North American Rocky Mountain Pine Beetle infestation. Am. J. Public Health, **102**: 818–827. doi:10.2105/AJPH.2011. 300520.

Emmel, C., Paul-Limoges, E., Bowler, R., Black, T.A., and Christen, A. 2014. Vertical distribution of carbon dioxide sources and sinks in a recovering mountain pine beetle-attacked lodgepole pine stand. Agric. For. Meteorol. **195–196**: 108–122. doi:10.1016/j.agrformet.2014.04.014.

Environment Canada. 2012. National inventory report, 1990–2010: greenhouse gas sources and sinks in Canada. Available from http://www.ec.gc.ca/ publications/A91164E0-7CEB-4D61-841C-BEA8BAA223F9/Executive-Summary2012_WEB-v3.pdf [accessed 6 May 2015].

Erbilgin, N., Ma, C., Whitehouse, C., Shan, B., Najar, A., and Evenden, M. 2014. Chemical similarity between historical and novel host plants promotes range and host expansion of the mountain pine beetle in a naïve host ecosystem. New Phytol. **201**: 940–950. doi:10.1111/nph.12573.

Faber, S., Costanza, R., Childers, D.L., Erickson, J., Gross, K., Grove, M., Hopkinson, C.S., Kahn, J., Pincetl, S., Troy, A., Warren, P., and Wilson, M. 2006. Linking ecology and economics for ecosystem management. BioScience, **56**: 121–133. doi:10.1641/0006-3568(2006)056[0121:LEAEFE]2.0.CO;2.

Fall, A., Shore, T.L., Safranyik, L., Riel, W.G., and Sachs, D. 2004. Integrating landscapescale mountain pine beetle projection and spatial harvesting models to assess management strategies. *In* Challenges and Solutions: Proceedings of the Mountain Pine Beetle Symposium, Kelowna, BC, October 30–31, 2003. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Information Report BC-X-399. pp. 114–132.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., and Gustafsson, L. 2014. Can retention forestry help conserve biodiversity? A meta-analysis. J. Appl. Ecol. **51**: 1669–1679. doi:10. 1111/1365-2664.12289.

Ferrari, M.R., Miller, J.R., and Russell, G.L. 2007. Modeling changes in summer temperature of the Fraser River during the next century. J. Hydrol. **342**: 336–346. doi:10.1016/j.jhydrol.2007.06.002.

Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negroìn, J.F., and Nowak, J.T. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For. Ecol. Manage. **238**: 24–53. doi:

10.1016/j.foreco.2006.10.011.

Fettig, C.J., Reid, M.L., Bentz, B.J., Sevanto, S., Spittlehouse, D.L., and Wang, T. 2013*a*. Changing climates, changing forests: a western North American perspective. J. For. **111**: 214–228. doi:10.5849/jof.12-085.

Fettig, C.J., Munson, A.S., Grosman, D.M., and Bush, P.B. 2013*b*. Evaluations of emamectin benzoate and propiconazole for protecting individual *Pinus contorta* from mortality attributed to colonization by *Dendroctonus ponderosae* and associated fungi. Pest Manage. Sci. **70**: 771–778. doi:10.1002/ps.3612.

Fettig, C.J., Gibson, K.E., Munson, A.S., and Negrón, J.F. 2014. Cultural practices for prevention and mitigation of mountain pine beetle infestations. For. Sci. **60**: 450–463. doi:10.5849/forsci.13-032.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, J., Monfreda,

C., Patz, J.A., Prentice, I.C., Ramankutty, N., and Snyder, P.K. 2005. Global consequences of land use. Science, **309**: 570–574. doi:10.1126/science.1111772.

Forest Practices Board. 2007. The effect of mountain pine beetle attack and salvage harvesting on streamflows. Forest Practices Board, Victoria, BC, Special Investigation, FPB/SIR/16.

Gillette, N.E., Wood, D.L., Hines, S.J., Runyon, J.B., and Negrón, J.F. 2014. Consequences of mountain pine beetle treatment decisions. For. Sci. **60**: 527–538. doi:10.5849/forsci.13-040.

Griffin, J.M., Turner, M.G., and Simard, M. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. For. Ecol. Manage. **261**(6): 1077–1089. doi:10.1016/j.foreco.2010.12. 031.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J.,

Lindenmayer, D.B., Lohmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Severdrup-Thygenson, A., Volney, W.J.A., Wayne, A., and Franklin, J.F. 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience, **62**: 633–645. doi:10.1525/bio.2012.62.7.6.

Hamer, D. 1996. Buffaloberry [*Shepherdia canadensis* (L.) Nutt.] fruit production in fire-successional bear feeding sites. J. Range Manage. **46**: 520–529.

Hansen, E.M. 2014. Forest development and carbon dynamics after mountain pine beetle outbreaks. For. Sci. **60**(3): 476–488. doi:10.5849/forsci.13-039.

Hansen, E.M., Amacher, C.M., Miegroet, H.V., Long, J.N., and Ryan, M.G. 2015. Carbon dynamics in central US Rockies lodgepole pine type after mountain pine beetle outbreaks. For. Sci. **61**: 665–679. doi:10.5849/forsci.14-094.

Hart, S.J., Schoennagela, T., Veblena, T.T., and Chapmana, T.B. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proc. Natl. Acad. Sci. U.S.A. **112**: 4375–4380. doi:10.1073/pnas. 1424037112.

Harvey, B.J., Donato, D.C., and Turner, M.G. 2014. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proc. Natl. Acad. Sci. U.S.A. **111**: 15120–15125. doi:10.1073/pnas. 1411346111.

Hassan, M., Hogan, D., and Bird, S. 2008. Mountain pine beetle impacts on channel morphology and woody debris in forested landscapes. Natural Resources Canada, MPB Working Paper 2008-07.

Hawkins, C.D.B., Dhar, A., Balliet, N.A., and Runzer, K.D. 2012. Residual mature trees and secondary stand structure after mountain pine beetle attack in central British Columbia. For. Ecol. Manage. **277**: 107–115. doi:10.1016/j.foreco. 2012.04.023.

Hawkins, C.D.B., Dhar, A., and Balliet, N. 2013. Radial growth of residual overstory trees and understory saplings after mountain pine beetle attack in centralBritishColumbia.For.Ecol.Manage.**310**:348–356.doi:10.1016/j.foreco. 2013.08.035.

Hélie, J.F., Peters, D.L., Tattrie, K.R., and Gibson, J.J. 2005. Review and synthesis of potential hydrologic impacts of mountain pine beetle and related harvesting activities in British Columbia. Canadian Forest Service, Victoria, BC, MPB Working Paper 2005-23.

Hicke, J.A., Johnson, M.C., Hayes, J.L., and Preisler, H.K. 2012*a*. Effects of bark beetle-caused tree mortality on wildfire. For. Ecol. Manage. **271**: 81–90. doi: 10.1016/j.foreco.2012.02.005.

Hicke, J.A., Allen, C.D., Desai, A., Dietze, M.C., Hall, R.J., Hogg, E.H., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N., and Vogelmann, J. 2012*b*. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Glob. Chang. Biol. **18**: 7–34. doi:10.1111/j.1365-2486.2011.02543.x.

Hinch, S., and Mellina, E. 2008. Stream habitat and bull trout (*Salvelinus confluentus*) responses to MPB riparian salvage harvesting in north-central British Columbia. FIA–FSP Project Y091046.

Hoffman, C.M. 2011. Numerical simulation of crown fire hazard in bark beetle infested lodgepole pine forests. Ph.D. dissertation, University of Idaho.

Hopping, G.R., and Mathers, W.G. 1945. Observations on outbreaks and control of the mountain pine beetle in the lodgepole pine stands of western Canada. For. Chron. **21**(2): 98–108. doi:10.5558/tfc21098-2.

Jenkins, M.J., Hebertson, E., Page, W., and Jorgenson, C.A. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For. Ecol Manage. **254**: 16–34. doi:10.1016/j.foreco.2007.09.045.

Jenkins, M.J., Runyon, J.B., Fettig, C.J., Page, W.G., and Bentz, B.J. 2014. Interactions among the mountain pine beetle, fires, and fuels. For. Sci. **60**: 489–501. doi:10.5849/forsci.13-017.

Johannes, M.R.S., Kenney, A., Pouliotte, J., and Steele, D. 2007. Mountain pine beetle threats to salmon and fisheries resources. *In* Proceedings of the Pacific Salmon Foundation and Fraser Basin Council Workshop, January 30–31, 2007, Prince George, BC.

Johnson, S.L., and Jones, J.A. 2000. Stream temperature response to forest harvest and debris flows in western Cascades, Oregon. Can. J. Fish. Aquat. Sci. **57**(S2): 30–39. doi:10.1139/f00-109.

Jolly, W.M., Parsons, R.A., Hadlow, A.M., Cohn, G.M., McAllister, S.S., Popp, J.B., Hubbard, R.M., and Negroìn, J.F. 2012. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. For. Ecol. Manage. **269**: 52–59. doi:10.1016/j. foreco.2011.12.022.

Keville, M.P., Reed, S.C., and Cleveland, C.C. 2013. Nitrogen cycling responses to mountain pine beetle disturbance in a high elevation whitebark pine ecosystem. PLoS One, **8**(6): e65004. doi:10.1371/journal.pone.0065004.

Kimmins, J.P. 1987. Forest ecology. Macmillan Publishing Company, New York.

Klutsch, G.J., Battaglia, M.A., West, D.R., Costello, S.L., and Negrón, J.F. 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. West. J. Appl. For. **26**(3): 101–109.

Kovacic, D.A., Dyer, M.I., and Cringan, A.T. 1985. Understory biomass in ponderosa pine following mountain pine beetle infestation. For. Ecol. Manage. **13**: 53–67. doi:10.1016/0378-1127(85)90005-2.

Kulakowski, D., and Jarvis, D. 2011. The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: a look at the past century. For. Ecol. Manage. **262**: 1686–1696. doi:10.1016/j.foreco.2011.07.016.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature, **452**: 987–990. doi:10.1038/nature06777.

Lal, R., Lorenz, K., Hüttl, R.R.J., Schneider, B.U., and von Braun, J. 2013. Ecosystem services and carbon sequestration in the biosphere. Springer, Dordrecht, Netherlands.

Larkin, G.A., Slaney, P.A., Warburton, P., and Wilson, A.S. 1998. Suspended sediment and fish habitat sedimentation in central interior watersheds of British Columbia. Ministry of Environment, Lands and Parks, Watershed Restoration Management Report No. 7.

Larsen, T.A. 2012. The potential influence of mountain pine beetle (*Dendroctonus ponderosae*) control harvesting on grizzly bear (*Ursus arctos*) food supply and habitat conditions in Alberta. M.Sc. thesis, Department of Biological Science, University of Alberta, Edmonton, Alberta, Canada.

Lindenmayer, D.B., Burton, P.J., and Franklin, F.J. 2008. Salvage logging and its ecological consequences. Island Press, Washington, D.C.

Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., and Gustafsson, L. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conserv. Lett. **5**: 421–431. doi:10.1111/j.1755-263X. 2012.00257.x.

Litterman, B. 2013. What is the right price for carbon emissions? Regulation, Summer **2013**: 38–43.

Logan, J.A., and Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). Am. Entomol. **47**: 160–172. doi:10. 1093/ae/47.3.160.

Lotan, J.E., Brown, J.K., and Neuenschwander, L.F. 1985. Role of fire in lodgepole pine ecosystems. *In* Lodgepole pine: the species and its management. *Edited by* D. Baumgartner, R. Krebill, J. Arnott, and G. Weetman. Washington State University, Pullman, Washington. pp. 133–152.

Lynch, H.J., Renkin, R.A., Crabtree, R.L., and Moorcroft, P.R. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems, **9**: 1318–1327. doi:10.1007/s10021-006-0173-3.

Maclauchlan, L. 2006. Status of mountain pine beetle attack in young lodgepole pine stands in the central British Columbia: report prepared for the Chief Forester. B.C. Ministry of Forests and Range, Victoria, British Columbia.

Maloney, D. 2004. The effects of riparian harvesting on fish habitat and ecology of small headwater streams. Year-end Report, FIA–FSP Project R04-032.

Mann, A., Tam, C., Higgins, C., and Rodrigues, L. 2007. The association between drinking water turbidity and gastrointestinal illness: a systematic review. BMC Public Health, **7**: 256. doi:10.1186/1471-2458-7-256.

Martin, K., Norris, A., and Drever, M. 2006. Effects of bark beetle outbreaks on avian biodiversity in the British Columbia interior: implications for critical habitat management. B.C. J. Ecosyst. Manage. **7**: 10–24.

Mathys, A., Black, T.A., Nesic, Z, Nishio, G., Brown, M., Spittlehouse, D.L., Fredeen, A.L., Bowler, R., Jassal, R.S., Grant, N.J., Burton, P.J., Trofymow, J.A., and Meyer, G. 2013. Carbon balance of a partially harvested mixed conifer forest following mountain pine beetle attack and its comparison to a clearcut. Biogeosciences, **10**: 5451–5463. doi:10.5194/bg-10-5451-2013.

McCullough, D.G., Werner, R.A., and Neumann, D. 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annu. Rev. Entomol. **4**: 107–127. doi:10.1146/annurev.ento.43.1.107.

McFarlane, B.L., and Watson, D.O. 2008. Perceptions of ecological risk associated with mountain pine beetle (*Dendroctonus ponderosae*) infestations in Banff and Kootenay National Parks of Canada. Risk Anal. **28**: 203–212. doi:10.1111/j.15396924.2008.01013.x.

McFarlane, B.L., Stumpf-Allen, R.C.G., and Watson, D.O. 2006. Public perceptions of natural disturbance in Canada's national parks: the case of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Biol. Conserv. **130**: 340–348.

McIntosh, A.C.S., and Macdonald, S.E. 2013. Potential for lodgepole pine regeneration after mountain pine beetle attack in newly invaded Alberta stands. For. Ecol. Manage. **295**: 11–19. doi:10.1016/j.foreco.2012.12.050.

Meigs, G.W., Campbell, J.L., Zald, H.S., Bailey, J.D., Shaw, D.C., and Kennedy, R.E. 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere, **6**: article 118. doi:10.1890/ES15-00037.1.

Meitner, M., South, C., and Wieler, C. 2011. Post-mountain pine beetle recreational usage survey: project final report. BC Ministry of Forest, Lands and Natural Resource Operations, Victoria, B.C.

Meyers Norris Penny (MNP). 2015. BC forest industry: economic impact study. Available from http://www.cofi.org/wp-content/uploads/2015/01/bc_industry_ impact_01-2015.pdf [accessed 11 February 2016].

Meitner, M., Cluny, S., and Carossa, W. 2011. Post-mountain pine beetle recreational usage survey. Mid-term Timber Supply Report Appendix 8.

Mikkelson, K.M., Dickerson, E.R., McCray, J.E., Maxwell, R.M., and Sharp, J.O. 2012. Water quality impacts from climate-induced forest die-off. Nat. Clim. Change, **3**: 218–222. doi:10.1038/nclimate1724.

Mikkelson, K., Bearup, L.A., Maxwell, R.M., Stednick, J.D., McCray, J.E., and Sharp, J.O. 2013. Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects. Biogeochemistry, **115**: 1–21. doi:10.1007/s10533-013-9875-8.

Millennium Ecosystem Assessment (MEA). 2005. Ecosystems and human wellbeing: synthesis. Island Press, Washington, D.C.

Mitchell, D., Hobby, T., Brigham, T., Hamilton, E., and Robertson, S. 2006. Canadian non-timber forest products: strategies for sustainable management, community development and policy implementation. *In* Proceedings of the Sustainable Forest Management Network 2006 Conference, Sustaining Canada's Forests: Building Momentum, Edmonton, Alta., 20–22 June 2006, Discussion Forum 7.

Mitchell, R.G., Waring, R.H., and Pitman, G.B. 1983. Thinning lodgepole pine increases vigor and resistance to mountain pine beetle. For. Sci. **29**: 204–211.

Moola, F.M., and Mallik, A.U. 1998. Morphological plasticity and regeneration strategies of velvet leaf blueberry (*Vaccinium myrtilloides* Michx.) following canopy disturbance in boreal mixedwood forests. For. Ecol. Manage. **111**: 35–50. doi:10.1016/S0378-1127(98)00306-5.

Mooney, H.A., and Ehrlich, P.R. 1997. Ecosystem services: a fragmentary history. *In* Nature's services: societal dependence on natural ecosystems. *Edited by* G. Daily. Island Press, Washington, D.C. pp. 11–19.

Nealis, V., and Peter, B. 2008. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests. Canada Forest Service, Victoria, B.C., Information Report BC-X-417.

Negrón, J.F., and Fettig, C.J. 2014. Mountain pine beetle, a major disturbance agent in US western coniferous forests: a synthesis of the state of knowledge. For. Sci. **60**: 409–413. doi:10.5849/forsci.13-169.

Negroìn, J.F., Bentz, B.J., Fettig, C.J., Gillette, N., Hansen, E.M., Hayes, J.L., Kelsey, R.G., Lundquist, J.E., Lynch, A.M., Progar, R.A., and Seybold, S.J. 2008. US Forest Service bark beetle research in the western United States: looking toward the future. J. For. **106**: 325–331.

Nielsen, S.E., Munro, R.H.M., Bainbridge, E.L., Stenhouse, G.B., and Boyce, M.S. 2004. Grizzly bears and forestry: II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. For. Ecol. Manage. **199**: 67–82. doi:10.1016/j.foreco.2004.04.015.

Olivotto, T. 1999. Pine mushroom and timber production in the Cranberry Timber Supply Area. Northwest Institute for Bioregional Research, Smithers, B.C.

Page, W., and Jenkins, M.J. 2007. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. For. Sci. **53**: 662–674.

Page, W.G., Jenkins, M.J., and Runyon, J.B. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. Can. J. For. Res. **42**(8): 1631–1647. doi:10.1139/x2012-094.

Parks Canada. 2001. Resource conservation: Banff field unit. Report from the Field — 2011. Available from http://publications.gc.ca/collections/ collection_2012/pc/R61-87-2011-eng.pdf [accessed 30 May 2016].

Patriquin, M.N., Wellstead, A.M., and White, W.A. 2007. Beetles, trees, and people: regional economic impact sensitivity and policy considerations related to the mountain pine beetle infestation in British Columbia, Canada. For. Policy Econ. **9**: 938–946. doi:10.1016/j.forpol.2006.08.002.

Pec, G.J., Karst, J., Sywenky, A.N., Cigan, P.W., Erbilgin, N., Simard, S.W., and Cahill, J.F., Jr. 2015. Rapid increases in forest understory diversity and productivity following a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in pine forests. PLoS One, **10**(4): e0124691. doi:10.1371/journal.pone. 0124691.

Perovich, P., and Sibold, J.S. 2016. Forest composition change after a mountain pine beetle outbreak, Rocky Mountain National Park, CO, USA. For. Ecol. Manage. **366**: 184–192. doi:10.1016/j.foreco.2016.02.010.

Perrakis, D.D.B., Lanoville, R.A., Taylor, S.W., and Hicks, D. 2014. Modeling wildfire spread in mountain pine beetle-affected forest stands, British Columbia, Canada. Fire Ecol. **10**(2): 10–35. doi:10.4996/fireecology.1002010.

Potts, D.F. 1984. Hydrologic impact of a large scale mountain pine beetle (*Dendroctonous ponderosae* Hopkins) epidemic. J. Am. Water Resour. Assoc. **20**: 373–377. doi:10.1111/j.1752-1688.1984.tb04719.x.

Pousette, J. 2010. Secondary stand structure and its timber supply implication for mountain pine beetle attacked forests on the Nechako plateau of British Columbia. M.Sc. thesis, University of Northern British Columbia, Prince George, B.C.

Progar, R.A., Gillette, N.E., Fettig, C.J., and Hrinkevich, K.H. 2014. Applied chemical ecology of the mountain pine beetle. For. Sci. **60**(3): 414–433. doi:10.5849/ forsci.13-010.

Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S., Healey, M.C., Farrell, A.P., and Higgs, D.A. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. Trans. Am. Fish. Soc. **135**: 655–667. doi:10.1577/T05-023.1.

Reed, E.D., Ewers, E.B., and Pendall, E. 2014. Impact of mountain pine beetle induced mortality on forest carbon and water fluxes. Environ. Res. Lett. **9**: 105004. doi:10.1088/1748-9326/9/10/105004.

Rex, J., Krauskopf, P., Maloney, D., and Tschaplinski, P. 2009. Mountain pine beetle and salvage harvesting: small stream and riparian zone response in the Sub-Boreal Spruce Zone. BC Ministry of Forests and Range, Forest Science Program, Victoria, B.C., Extension Note 90.

Riel, W.G., Fall, A., Shore, T.L., and Safranyik, L. 2004. A spatio-temporal simulation of mountain pine beetle impacts on the landscape. *In* Challenges and Solutions: Proceedings of the Mountain Pine

Beetle Symposium, Kelowna, BC, 30–31, October 2003. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., Information Report BC-X-399. pp. 106–113.

Romme, W.H., Knight, D.H., and Fedders, J. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: effects on fuels and fire in lodgepole pine forest. *In* Proceedings of the Program of the Annual Meeting of the Ecological Society of America. Syracuse University, N.Y.

Rosenberger, R.S., and Smith, E.L. 1998. Assessing forest scenic beauty impacts of insects and management. USDA Forest Service, Forest Health Technology Enterprise Team (FHTET), Research Paper 98-08.

Rosenberger, S.R., Bell, A.L., Champ, A.P., Eric, M., and White, E.M. 2013. Estimating the economic value of recreation losses in Rocky Mountain National Park due to a mountain pine beetle outbreak. Western Economics Forum,

12(1): 31–39.

Saab, V.A., Latif, Q.S., Rowland, M.M., Johnson, T.N., Chalfoun, A.D., Buskirk, S.W., Heyward, J.E., and Dresser, M.A. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. For. Sci. **60**: 539–559. doi:10.5849/forsci.13-022.

Safranyik, L., and Carroll, A.L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *In* The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. *Edited by* L. Safranyik and B. Wilson. Natural Resources Canada, Victoria, B.C. pp. 3–66.

Safranyik, L., Shrimpton, D.M., and Whitney, H.S. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service, Pacific Forest Research Centre, Victoria, B.C., Forest Technical Report No. 1.

Schnorbus, M. 2011. A synthesis of the hydrological consequences of large-scale mountain pine beetle disturbance. Natural Resources Canada, Victoria, B.C., Mountain Pine Beetle Working Paper 2010-01.

Schoennagel, T., Veblen, T.T., Negron, J.F., and Smith, J.M. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS One, **7**(1): e30002. doi:10.1371/journal.pone.0030002.

Schowalter, T.D. 2012. Insect herbivore effects on forest ecosystem services. J. Sustain. For. **3**: 518–536. doi:10.1080/10549811.2011.636225.

Seip, D., and Jones, E. 2010. Response of woodland caribou to partial retention logging of winter ranges attacked by mountain pine beetle. Annual Report. FSP Project No. Y102010. BC Ministry of Forests, Prince George, B.C.

Sheppard, S., and Picard, P. 2006. Visual-quality impacts of forest pest activity at the landscape level: a synthesis of published knowledge and research needs. Landsc. Urban Plan. **77**: 321–342. doi:10.1016/j.landurbplan.2005.02.007.

Shore, L.T., Safranyik, L., Hawkes, C.B., and Taylor, W.S. 2006. Effects of the mountain pine beetle on lodgepole pine stand structure and dynamics. *In* The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. *Edited by* L. Safranyik and B. Wilson. Natural Resources Canada, Victoria, B.C. pp. 95–116.

Shore, T.L., and Safranyik, L. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Forestry Canada, Pacific Forestry Centre, Victoria, B.C., Information Report BC-X-336.

Shore, T.L., and Safranyik, L. 2004. Mountain pine beetle management and decision support. *In* Challenges and Solutions: Proceedings of the Mountain Pine Beetle Symposium, Kelowna, BC,

30–31 October 2003. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., Information Report BCX-399. pp. 97–105.

Simard, M., Romme, W., Griffin, J., and Turner, M.G. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol. Monogr. **81**: 3–24. doi:10.1890/10-1176.1.

Six, L.D., Biber, E., and Long, E. 2014. Management for mountain pine beetle outbreak suppression: does relevant science support current policy? Forests, **5**: 103–133. doi:10.3390/f5010103.

Statistics Canada. 2012. Aquaculture statistics 2011. Catalogue no. 23-222-X. Available from http://www.aquaculture.ca/files/documents/AquacultureStatistics2011.pdf [accessed 23 May 2015].

Stednick, J. 2007. Preliminary assessment of water quantity and water quality changes in beetle-killed catchments in north-central Colorado. *In* Mountain Pine Beetle and Watershed Hydrology Workshop: preliminary results from BC, Alberta and Colorado. *Edited by* T. Redding. pp. 27–28.

Steventon, J.D. 2015. Arboreal squirrel abundance in response to a gradient of mountain pine beetle attack in sub-boreal forests. J. Ecosyst. Manage. **15**(1): 1–12.

Stone, W.E., and Wolfe, M.L. 1996. Response of understorey vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. Vegetatio, **122**: 1–12. doi:10.1007/BF00052811.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., and Ransome, D.B. 2010. Greentree retention and life after the beetle: stand structure and small mammals 30 years after salvage harvesting. Silva Fenn. **44**: 749–774. doi:10.14214/sf.451.

Taylor, S.W., and Carroll, A.L. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective. *In* Challenges and Solutions: Proceedings of the Mountain Pine Beetle Symposium, Kelowna, BC, 30–31 October 2003. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., Information Report BC-X-399. pp. 41–51.

The Economics of Ecosystems and Biodiversity (TEEB). 2010. Mainstreaming the economics of nature: a synthesis of the approach, conclusions and recommendations of TEEB. Earthscan, London and Washington.

Trahan, N.A., Dynes, E.L., Pugh, E., Moore, D.J.P., and Monson, R.K. 2015. Changes in soil biogeochemistry following disturbance by girdling and mountain pine beetles in subalpine forests. Oecologia, **177**: 981–995. doi:10.1007/s00442-0153227-4.

Walton, A. 2013. Provincial-level projection of the current mountain pine beetle outbreak: update of the infestation projection based on the provincial aerial overview surveys of forest health conducted from 1999 through 2012 and the BCMPB model (year 10). BC Ministry of Forests, Lands and Natural Resource Operations. Available from https://www.for.gov.bc.ca/ftp/hre/external/ !publish/web/bcmpb/year9/BCMPB.v9.BeetleProjection.Update.pdf [accessed 14 April 2015].

Wong, C. 2008. Environmental impacts of mountain pine beetle in the Southern Interior. British Columbia Ministry of Environment, Prince George, BC. Available from http://www.sibacs.com/wp-content/uploads/2009/02/environmental-impactsreport-final.pdf [accessed 16 May 2015].

Wulder, M.A., Ortlepp, S.M., White, J.C., Coops, N.C., and Coggins, S.B. 2009. Monitoring the impacts of mountain pine beetle mitigation. For. Ecol. Manage. **258**: 1181–1187. doi:10.1016/j.foreco.2009.06.008.

Xue, D., and Tisdell, C. 2001. Valuing ecological functions of biodiversity in Changbaishan Mountain Biosphere Reserve in Northeast China. Biodivers. Conserv. **10**(3): 467–481. doi:10.1023/A:1016630825913.

Zwickel, H. 2012. Sport fishing in Alberta 2010: summary report from the eighth survey of recreational fishing in Canada. Alberta Sustainable Resources Development, Fisheries Management Branch, Edmonton, Alta.

Table 1. List of ecosystem services (ES) provided by pine forests mpacted by mountain pine beetle (MPB) in western Canada by ES category (provisioning, regulating, supporting, and cultural).

Ecosystem Service	Ecosystem function impacted by MPB	Impact intensity		Knowledge gap
		Salvaged stands	Unsalvaged stands	
Provisioning				
Raw Materials: timber	Natural resources primary production loss	-----	---	No
Water Supply	Change in storage and retention of water	---	-	Yes
Food: other forest foods	Natural resources secondary production gain	---	++	Yes
Regulating				
Climate regulation: carbon storage	Regulation of global temperature, precipitation & other climate processes	--	-/+	Yes
Sedimentation and water purification: water quality	Sedimentation and nutrient leaching to nearby streams. Increased chemical compounds in water	---	-	Yes
Fire regulation: forest fire	Ecosystem responses to extreme events	+	-/+	Yes
Supporting				
Biodiversity, genepool and life cycle maintenance	Terrestrial and aquatic species	---	+++	Yes
Nutrient cycling	Support for the growth of living organisms	----	--	Yes
Cultural				
Tourism and recreation	Trail closures, access & visitation	--	-	No
Aesthetic or scenic beauty	Change in visual quality	---	---	Yes

Note: Impact intensity was based on a qualitative assessment where intensity of plus (+) or minus (−) indicates the degree of positive and negative effects, respectively, on the particular ecosystem service, and together plus and minus (+/−) indicates effect in doubt.