*forests*

MDPI

*Review*

# Aftermath of Mountain Pine Beetle Outbreak in British Columbia: Stand Dynamics, Management Response and Ecosystem Resilience

**Amalesh Dhar [1,*,†], Lael Parrott [1] and Christopher D.B. Hawkins [2]**

[1] Okanagan Institute for Biodiversity, Resilience, and Ecosystem Services (BRAES), University of British Columbia, Okanagan Campus, 1177 Research Road, Kelowna, BC V1V 1V7, Canada; lael.parrott@ubc.ca

[2] Yukon Research Centre, Whitehorse, YK Y1A 5K4, Canada; chawkins@yukoncollege.yk.ca

* Correspondence: amalesh@ualberta.ca; Tel.: +1-780-492-6538; Fax: +1-780-492-4323

† Present address: Department of Renewable Resources, University of Alberta, 847 General Services Bldg, Edmonton, AB T6G 2H1, Canada.

Academic Editors: Jarmo K. Holopainen and Timothy A. Martin
Received: 9 June 2016; Accepted: 2 August 2016; Published: 5 August 2016

**Abstract:** The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) has infested and killed millions of hectares of lodgepole pine (*Pinus contorta* var. *latifolia Engelm*) forests in British Columbia, Canada, over the past decade. It is now spreading out of its native range into the Canadian boreal forest, with unknown social, economic and ecological consequences. This review explores the ramifications of the MPB epidemic with respect to mid-term timber supply, forest growth, structure and composition, vegetation diversity, forest fire, climate change, and ecosystem resilience. Research confirms that, in British Columbia, all of these variables are more significantly impacted when salvage logging is used as management response to the outbreak. We conclude that appropriate management in response to MPB is essential to ensuring ecologically resilient future forests and reliable mid-term timber supplies for affected human communities. We highlight knowledge gaps and avenues for research to advance our understanding in support of sustainable post-disturbance forest management policies in British Columbia and elsewhere.

**Keywords:** climate change; forest disturbance; forest resilience; mid-term timber supply; stand dynamics

---

## 1. Introduction

The mountain pine beetle (MPB) (*Dendroctonous ponderosae* Hopkins) is part of the natural system in British Columbia's pine forests and it helps to maintain biological diversity and functionally healthy landscapes [1]. The MPB can be found in pine forests from western Canada to northern Mexico [2]. Generally, lodgeple pine (*Pinus contorta* var. *latifolia Engelm*) is the most common host, but other pine species including ponderosa pine (*P. ponderosa* Laws), whitebark pine (*P. albicaulis* Engelm.), western white pine (*P. monticola* Dougl.), limber pine (*P. flexilis* James), coulter pine (*P. coulteri* D. Don) and Scots pine (*P. sylvestris* L.) are also suitable hosts [3]. The female beetles lay their eggs along the sides of vertical galleries 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 [3]. In addition, beetles are also vectors of three blue stain symbiotic fungi (*Grosmannia clavigera* Robinson-Jeffrey & R.W. Davidson, *Ophiostoma montium* (Rumbold) von Arx., and *Leptographium longiclavatum* Lee, Kim and Breuil), which contribute to beetle success [4–6]. Although MPB broods can be reared without their symbiotic fungi [7], the fungi have a positive influence on the survival of beetle broods by (i) exhausting tree defenses during mass-attack [8]; (ii) expediting the development of immature beetles [9]; and (iii) increasing phloem nutrients [10–12].

Beetles 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 [3]. Generally large and slow growing trees are the preferred beetle host due to their inability to resist the establishment of adults in the phloem layer [13,14]. Control or prevention of beetle infestation is particularly difficult as beetles spend most of their life cycle protected under the bark [15]. However, in addition to extreme winter temperatures ($<-40$ °C) [3], unseasonable temperatures in the early or late development stage of the beetle could lead to high mortality [16].

An outbreak is dependent on the size of the beetle population, climate and degree of susceptible stands distributed over the landscape and stand characteristics such as species composition, diameter, age, and stand density [17]. Based on dendroecological studies, four to five MPB outbreaks occurred in BC during the last century, with an average duration of ~10 years [18,19], while in the northern Rocky Mountains of the United States, MPB outbreaks occur every 20 to 40 years and typically last for ~6 years [20]. The rate of spread and severity of the current outbreak is the largest recorded in the history of Canada, infesting >20 million hectares of pine forest in western Canada [21,22]. Climate change (winter minimum temperatures that are too warm to cause beetle larval mortality) and effective forest management (e.g., harvest regulation, fire suppression that maintained an abundant mature pine tree population across the landscape leading to homogenous stand structures) are considered major factors which expedited the expansion of MPB outbreaks in BC and the spread east of the Rocky Mountains to boreal jack pine (*Pinus banksiana* Lamb.) forests [19–22]. Typically, MPB attack large or old individuals (diameter >20 cm or >60 years of age) of pine. However, due to the severity of the current outbreak, MPB even attacked young pine trees (diameter $\leqslant$7.5 cm or $\leqslant$13 years age) if no mature trees were available [23]. MPB impacts are far reaching and have undoubtedly altered stand and landscape structure as well as having severe consequences on BC's interior forest industry. The mid-term timber supply (portion of the timber that would be available for harvest within the middle of the normal management cycle which is generally 30–70 years in interior BC) [24] has been especially affected, as well as different ecosystem services (water supply, non-timber forest, products, habitat suitability, scenic beauty, carbon storage, nutrient cycling etc.) provided by the forest [25].

In spite of significant advancement in research on management of forest disturbance [3,14,17], 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 (monosodium methanearsonate (MSMA)), semiochemicals, or pheromones used on trap trees [26–28]. Unfortunately, the effectiveness of some of these direct management approaches (sanitation, insecticide, semiochemicals) does 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 [26,28–30]. Thus, with the high intensity of attack, management efforts were eventually shifted to salvage logging (clear cut) operations to capture as much of the economic value of dead timber as possible before the wood deteriorated and may slow the spread of beetles to other areas. While large-scale salvage logging in some areas may be an appropriate economic response, harvesting all the killed timber is not possible, nor is it feasible or practical, and may be unsound ecologically due to its negative impact [23,31–33]. Regardless of the choice of mitigation strategy, forest managers must conscientiously continue to conserve forest values such as biodiversity, hydrology, soil, as well as stand structure and age class distribution [32]. The impacts of this colossal outbreak, coupled (compounded) with large-scale salvage operations will likely lead to conditions outside the natural range of disturbances that these ecosystems have experienced historically [14,31,33]. Information regarding the response of pine-dominated ecosystems to disturbances such as fire and harvesting is available [2,34–36]; however, it is still unclear whether stand dynamics will respond similarly with respect to a large-scale beetle epidemic. Therefore, understanding how MPB-attacked stands will develop and characterize the future landscape is essential for assessing the impending impacts on ecological and socioeconomic conditions.

Considerable studies have been conducted to determine the post beetle stand dynamics across the MPB impacted areas in western Canada. However, this information needs to be gathered, synthesized, and presented in such way that it is widely available and understandable to managers, practitioners, and researchers alike. We have, therefore, compiled this review to describe post beetle dynamics across the landscape in western Canada with an emphasis on BC. The outcome of this review will assist the initiation of sustainable forest management policies for MPB impacted areas in BC and elsewhere.

## 2. Stand Structure and Composition

From different studies, it is well documented that MPB outbreaks play an important role in directing ecological process and the dynamics of lodgepole pine forests [1,14,23,37–40]. Moreover, beetle infestations are viewed as stand-releasing disturbances that favour the release of existing suppressed and understory trees which then form a new forest (e.g., [1,18,39–42]). In the absence of fire, MPB outbreaks exert widespread influence upon stand succession processes in favour of shade tolerant or semi shade tolerant species in even-aged pine forests [1,37,39,43]. However, forest management practices before (e.g., fire suppression) and after (e.g., salvage logging) beetle attack may also play a vital role in the composition and size structure of understory and overstory species [33]. It is well established that structure and compositional development of salvage-logged (equivalent to clear cut) stands are significantly different from those of unsalvaged stands [32,44] as artificial regeneration with planting of nursery-grown tree seedlings is the basis of reforestation activity. In BC, nursery-grown tree seedlings such as lodgepole pine or hybrid spruce (*Picea glauca* Moench Voss × *Picea engelmannii* Parry) or subalpine fir (*Abies lasiocarpa* Hook. Nutt.) are used to facilitate the reforestation of salvage logged stands [45]. Stands developing from salvage-logged areas may thus have a simplified stand structure and composition as well as lower plant species richness and/or diversity as compared to unsalvaged forest left to naturally regenerate [32,46–50].

In unsalvaged stands, residual stand structure and composition play a vital role in development of the future forest [23,32,44]. Although the forests of central BC appear to have been devastated by the mountain pine beetle, studies of residual stand structure in many locations revealed that this was not the case for unsalvaged stands, as abundant residual green trees, regenerating saplings and seedlings of currently acceptable commercial tree species remain in the stands [51–55]. The recruitment rate and species composition of new regeneration after MPB attack are variable across the landscape (different combinations of species and densities). Several recent studies reported successful recruitment with abundant regeneration beneath the tree layer after MPB attack [40,53–58] while others reported a slow recruitment process with substantially lower regeneration density [1,21,59]. However, Amoroso et al. [55] concluded that ingress of natural regeneration was slow in the first few years after MPB attack but there was a strong pulse of recruitment 10–20 years post disturbance. This could be the main the reason why some of the areas had low levels of recruitment. In addition, poor substrates and soil moisture, or availability of viable seed sources may also interrupt seedling recruitment [21,59].

Considering species composition, MPB-attacked forests are undergoing substantial conversion—moving from lodgepole pine to more shade-tolerant species in most areas of BC [43,54,55,59,60]. Shade tolerant subalpine fir and interior spruce are the most dominant understory species [1,54,55,59,60] followed by low-to-moderate shade tolerant species such as lodgepole pine and Douglas-fir [1,40,61]. This implies that MPB-caused mortality results in the rapid conversion of stands from lodgepole pine to shade-tolerant conifers (i.e., subalpine fir, interior spruce) [60,62] and accelerates the conversion of even-aged stands to uneven-aged stands [23,37,55].

## 3. Growth Response of Residual Live Trees

Due to MPB attack, forest changes will primarily be related to species abundance, composition and condition of residual secondary structure/trees [39,40,63]. As attacked trees die and more light reaches to the forest floor, advanced regeneration [20,64] and understory vegetation [46] display enhanced growth rates [42,55]. The radial growth rate depends on the amount of MPB-induced mortality [40] as well as the abundance and condition (vigour) of residual overstory and understory species [39,62]. Previous studies suggested that enhanced radial growth of the residual overstory generally started within three to five years of MPB attack [2]. Temporally, this is the grey stage of the stand (the grey stage follows the red stage (needles turn red and are still on the tree) and the needles turn grey and fall off the tree). Studies showed that the residual overstory grows at rates similar to [1,39,65] or greater than [66] trees that have never been suppressed. After the death of larger pine trees, healthy vigorous understory species exhibited increased radial growth compared to healthy overstory trees, although the extent of response varied among species and sites [42,55]. Generally, after the beetle attack, shade tolerant species (i.e., Douglas-fir (*Pseudotsuga menziesii* Mirbel. Franco); *Picea glauca* (Moench) Voss × *P. englemanii* Parry) demonstrated the greatest radial growth among understory species whereas shade intolerant species (i.e., lodgepole pine, trembling aspen (*Populus tremuloides* Michx.)) had the best growth response among overstory trees and in most cases, the degree of radial growth increased with increased pine mortality [42,55]. Considering the mean annual growth response, both residual overstory and understory trees species showed variable growth responses [42,55,67] and in some instances reached up to 400% from the pre-MPB conditions [67].

Generally, MPB attacks older trees (>60 years of age) and if we consider the growth pattern of pine trees, it reveals that peak productivity can be achieved 24–60 years after stand development and declines thereafter to 16%–48% of maximum values by the age of 200–350 years [68–70]. Therefore, disturbance caused by MPB "resets" the pine development to an earlier and possibly more productive stage and killed pine volume can be offset by the increased growth [42,55,67,68].

## 4. Mid-Term Timber Supply

The current MPB epidemic has already killed a cumulative total of 723 million $m^3$ of pine (53% of the total merchantable pine volume) in BC and approximately 752 million $m^3$ (56%) will likely be killed by 2018, in addition to another 2% by 2023 [22]. As a result, the BC Ministry of Forests increased the allowable annual cut (AAC) by 14.5 million $m^3$ from the pre-outbreak AAC level to capture as much economic value from the resource available as possible [71]. The AAC in some forest districts (e.g., Vanderhoof and Quesnel) has been increased more than twofold the pre-outbreak levels [72]. This means timber previously allotted for logging in the coming decades is instead being harvested over just a few years in the near term. It was anticipated that the increased AAC could last only 5 to 15 years due to a gradual deterioration in wood quality (shelf life varies with climate) of beetle-killed trees, accessibility, location, lack of milling facilities, and market conditions. With such a loss in useable timber stock, it is inevitable that sustainable levels of harvesting will have to be adjusted downward after the pine beetle outbreak, especially in timber supply areas heavily dependent on pine trees. It was estimated that there will be a precipitous drop of approximately 12.6 million $m^3$ in the province and approximately 75% in central BC (Prince George forest district) below pre-outbreak levels [71,73]. This AAC drop is projected to last for several decades because a forest requires 60–80 years to regenerate as a mature stand. Moreover, a significant number of young lodgepole pine stands have been attacked as well, and they were generally considered non-susceptible to the mountain pine beetle [72]. This implies that the pine beetle outbreak and exacerbated beetle-induced mortality and salvage uplifts constitute a dearth of mature forest habitat and ecosystem services as well as a mid-term timber supply decline. However, the overall impact on mid-term timber supply could be different depending on the management policy.

Several studies have revealed that a large percentage of MPB-impacted unsalvaged stands have enough (well-spaced, ⩾900 healthy stems $ha^{-1}$ >4 m in height or 700 stems $ha^{-1}$ >6 m in height) or basal area (~10 $m^2 \cdot ha^{-1}$) residual secondary structure (seedling, sapling and mature trees that survived after MPB attack) that could provide at least 150 $m^3 \cdot ha^{-1}$ of timber within thirty years (mid-term) of the MPB attack [23,51,52,54,67]. In central BC (Prince George forest district with an estimated area of 55,000 $km^2$), a severely MPB impacted area, Hawkins et al. [54] reported that depending on stand age, 44%–98% of attacked stands have enough secondary stand structure (sufficient stems ⩾ 900 stem $ha^{-1}$

> 4 m height and < 7.5 cm DBH) to contribute to the mid-term timber supply. In this assessment they did not include residual mature trees (DBH > 7.5 cm); if these trees were included, then the overall percentage would be much higher than indicated in the report. Similarly, Dhar et al. [67] reported that the vast majority of stands had greater, and often much greater, than 10 $m^2 \cdot ha^{-1}$ basal area of residual secondary structure (>4 cm DBH) in the post-beetle condition. This could easily provide mid-term timber supply within the desired time frame. In another study, Coates et al. [51] reported that only 20%–25% of stands needed some level of management intervention to achieve the mid-term timber supply goal. Even though the climate in BC is exceptionally variable, for most of the unsalvaged stands, mid-term timber supply shortfalls may not be a large concern [51,52,54] as previously projected [74].

The modelling approaches for the post beetle stand condition also revealed that a great proportion of MPB attacked stands have the potential to contribute to mid-term timber supply without further management activities [54,75]. Different types of models such as SORTIE-ND, PrognosisBC and their hybrids are mainly used to predict the dynamics of MPB-attacked stands in BC. Among them, SORTIE-ND is intensively applied to predict future or mid-term timber supply analysis across BC [51,54,75–78]. Based on projections by Hawkins et al. [54], stands with a minimum of 900 stems/ha (tree > 4 m height but < 7.5 cm DBH) of residual secondary stand structure can reach minimum merchantable volumes (150 $m^3 \cdot ha^{-1}$) in most of the age classes within 30 years after MPB attack. A similar result was also reported by Coates [75] in central BC. In another study, Coates et al. [51] indicated that stands with healthy, vigorous, and well-spaced advanced regeneration may develop rapidly following MPB attack and can contribute harvestable volumes of 200–300 $m^3 \cdot ha^{-1}$ within 25–40 years, which is greater than target timber production (150 $m^3 \cdot ha^{-1}$) for MPB-infected stands in BC. Similarly, Pousette [78] showed that a significant number of MPB killed stands in central BC can contribute mid-term merchantable timber within 30 years of MPB attack. In an earlier study Coates and Hall [76], suggested that after MPB-induced pine mortality, residual spruce in well-stocked stands with good basal area recovered to pre-attack basal areas within 50 years in two of four experimental stands in BC. For both mature and immature stands, Runzer et al. [77] suggested that the best option for MPB-impacted stands would be to allow the stand to develop naturally without intervention and harvest them to assist with mid-term timber supply. Likewise, field inventories also suggested that a significant number of MPB-attacked stands have the potential to contribute to mid-term timber supply without further management. Moreover, retention of stands with suitable residual stems can shorten rotation age greatly [52] compared to starting a new plantation after logging.

Finally, it has been recommended that if there is a need to continue salvage logging, then those stands which do not meet the mid-term timber supply minimum volume requirement should be selected and stands or portions of stands that will be economically viable through the mid-term should be retained [52]. This could be accomplished using partial cutting, by selectively logging the dead and dying pine from mixed stands. Leaving economically viable trees such as Douglas-fir or clumps of spruce and fir can compensate for a portion of mid-term timber in the decades after the pine is gone. However, the challenge after catastrophic forest disturbances is to strategically assess what should and should not be harvested in the short and medium terms. The goal is to create the most favourable timber supply and habitat supply forecast possible where management decisions come from integrated approaches by considering ecological, economical and societal values.

## 5. Forest Fire

Generally, it is hypothesized that MPB-induced tree mortality affects fire behavior by altering the flammability, continuity, and structure of fuels [79–82]. Moreover, the fuel profile such as surface, ladder, and crown fuels are expected to change with time since outbreak, potentially altering fire behavior and fire risk. After tree death, needles fade to red within a year of attack (red stage) and risks of ignition, torching, and canopy fire are expected to increase due to lower leaf moisture content (10 times lower in foliar moisture content compared to green needles), non-fiber carbohydrates and fats, which increase flammability [83,84]. Approximately 3 to 10 years (gray stage) after the beetle attack, trees drop their needles and twigs and become exposed in the upper crown [81], which likely increases the forest floor fuels [81,82]. Therefore, it is expected that surface fires will be more likely to spread into the canopy during the gray stage [85] and salvage logging is a recommended method of forest management to reduce the fire hazard [80–82]. However, MPB and its impacts on fuel accumulation and subsequent fire hazard are poorly understood: some studies have suggested higher probability or severity of fire following beetle outbreak [66,79,80], while others suggest a decreased fire probability [2,86], or no evidence of any relationship between MPB and active fire [34–36,87–89]. Based on an extensive literature review, Jenkins et al. [80] concluded that both rates of fire spread and fire-line intensities were higher in the current outbreak's stands than in endemic stands. Similarly, Lynch et al. [79] reported that MPB mortality in the mid-1970s increased the odds of burning in 1988 by 11% over unaffected areas in Yellowstone National Park, USA, whereas Alfaro et al. [2] suggested that there was no significant relationship in the frequency of beetle outbreak related to fire frequency in BC and they also found a positive relationship between MPB attack severity and less frequent fire. Similarly, Simard et al. [86] reported that the MPB outbreak in Greater Yellowstone may reduce the probability of active crown fires in the short term (up to 35 years after a beetle outbreak) by thinning lodgepole pine canopies. Likewise, a recent study in western USA claimed that the observed effect of MPB infestation on the area burned in 2002–2013 appears negligible at broad spatial extents [36]. Meigs et al. [89] claimed that following MPB outbreak, fire likelihood is neither higher nor lower than in non-MPB-affected forests in the Pacific Northwest of USA. Many studies emphasize the importance of climate rather than fuels as the primary driver of wild fires [34,35,87,90]. According to these studies, weather conditions such as extremely dry, gusty conditions with a sustainable ignition event and topography are the main driving factors in the occurrence of forest fire as opposed to MPB. There is thus no clear conclusion about the interaction of MPB-induced mortality and forest fire, and the debate persists. Further comprehensive study is required to answer this question by keeping in mind that the science of fire behaviour is very complex as many factors can influence how a fire will act and there are a number of unknowns when it comes to predicting fire behaviour in MPB infested stands.

## 6. Carbon Dynamics

Empirical and theoretical evidence suggests that MPB disturbances may not necessarily decrease cumulative carbon (C) productivity (i.e., total productivity over multiple years to decades). In fact, intermediate- severity disturbances (e.g., MPB) may accelerate, maximize, or even regulate ecosystem cycling and production [66,91,92]. However, there is ongoing debate about the impact of MPB on carbon dynamics due to the variability in research findings among the different studies [93–100]. Some studies reported that the MPB outbreak has a direct impact on carbon dynamics as tree mortality reduces the rate of forest carbon uptake and increases future emissions by excessive heterotrophic respiration and thus forests are being converted from net carbon sinks to carbon sources [93–95,101]. According to Kurz et al. [94], net greenhouse gas production over 21 years will be 990 Mt carbon dioxide equivalents ($CO_2$e) in MPB-impacted areas in BC, which will affect the carbon dynamics and exacerbate global climate change. A similar observation was also reported by Foley et al. [93]. However, flux tower-based observations and recent modelling conclude that MPB-killed forests are not changing from net carbon sinks to net carbon sources [96,97,102,103]. In fact, the healthy residual trees in MPB killed stands are sequestrating carbon at higher rates due to the rapid change of forest structure and composition [96,99–102]. Based on a recent study, Arora et al. [103] estimated that the current MPB outbreak in BC's forests could accumulate 328 Mt less carbon by 2020 while changing climate and increasing atmospheric $CO_2$ concentration could enhance carbon uptake equal to a cumulative sink of around 900–1060 Mt C, which is almost three times higher than the total loss. A comparable result has also been reported from field-based growth dynamics studies [42,55,67]. All of these studies report that residual tree species showed enhanced radial growth after beetle attack, leading to rapid carbon uptake by the residual tree species that compensates for losses due to tree mortality. Therefore, it can be suggested that the overall MPB impact on carbon dynamics is not as severe as previously predicted [93–95]; in fact, frequent moderate-severe MPB disturbances may stimulate C productivity of the forest stands [68,103].

## 7. Species Range Expansion

Climate change projections predict that a large portion of BC's central interior is expected to become drier while the northeastern portion is projected to become wetter [104]. This will influence species' geographic ranges, with species shifting northward and to higher elevations as well as impacting primary ecosystem processes like succession and disturbance [105]. The current climatic change projections suggest that many BC tree species' (i.e., *Larix occidentalis* Nutt., natural hybrids of *Picea englemannii* and *Picea gluca*; *Abies lasiocarpa* (Hooker) Nuttall, *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* Donn ex D.Don) distributions are predicted to shift their geographic ranges and some of these species are already found in the understory of MPB-impacted pine dominant forests [104,105]. MPB outbreaks may facilitate the shift of geographic distribution for those species by opening gaps in the forest canopy and breaking the "biological inertia" [106] of the mature pine trees that have been in holding for a long time. This opening of the canopy thus potentially permits the establishment of climatically better adapted trees present in the understory layer. Although such species could, in theory, be planted after salvage logging as a means of assisting range shifts, knowing which species to plant would require considerable research effort.

## 8. Biodiversity

The current MPB outbreak has direct impact on species richness and diversity for understory and herbaceous flora and fauna, [46,54,55,60,107–109] as MPB-caused mortality emulates a thinning from above, which allows more growing space (light, water, nutrients, etc.) for understory vegetation [43]. Details of MPB impact on vegetation diversity are discussed in the species composition and ecosystem resilience sections of this manuscript; thus, this section only treats the impact of MPB outbreaks on wildlife species. Various studies have revealed that MPB outbreaks have either direct (altering food and forage availability), indirect (altering habitat suitability), or mixed impacts on wildlife [110–112]. According to Martin et al. [111], bird species richness did not decline in stands having up to 60% pine mortality but showed a strong negative impact when mortality exceeded 75% [113]. Drever et al. [114], however, reported that the percent of red-attacked pines positively correlated to species richness of woodpeckers and negatively correlated to richness of other forest birds. In another study, Walters et al. [115] found that the abundance of tree sap eater migratory northern flickers (*Colaptes auratus* L.) and red-naped sapsuckers (*Sphyrapicus nuchalis* B.) decreased in MPB-killed stands. Similarly, Bonnot et al. [116] reported that wildlife species that depend on the forest cover showed less abundance when the dead trees drop their foliage. On the contrary, the occurrence and abundance of shrub species are strongly associated with abundance of many small mammals such as Trowbridge's shrew (*Sorex trowbridgii* B.) and Pacific water shrew (*S. bendirii* M.) [115] and well as with ungulate species that browse the new growth. Lastly, the management response to an MPB-impacted stand will also affect fauna. Salvaged stands, for example, will lose significant understory structure, modifying forage availability and habitats. Impacts of salvage logging also extend to the aquatic environment, causing increased sedimentation of rivers, modified flow regimes, and increased water temperatures. All of these impacts have been shown to affect fish habitat and spawning grounds [117–120]. Fully documenting the response of flora and fauna to MPB outbreaks and subsequent management interventions would require detailed and long-term studies across different geographic locations.

## 9. Ecosystem Resilience

Ecological resilience is the capacity of an ecosystem to maintain its identity, functions, and processes after disturbance [121]. Resilience of managed forest ecosystems can be enhanced by management actions that maintain the complexity of forest structure and dynamics from the stand to landscape scale [122,123]. Natural disturbances, when they occur within the natural range of variation for a particular ecosystem, serve to increase forest complexity by creating stand and landscape scale heterogeneity and can thus promote forest resilience. Forest management and harvesting that create patchy mosaics of even-aged stands can also contribute to landscape scale heterogeneity, while selective harvesting, for example, can lead to stand scale heterogeneity. Such interventions, that promote complex forest structure, may increase forest resilience to disturbance and environmental change [123]. However, management actions such as large-scale replanting of a single species or fire suppression, as well as unprecedented levels of natural disturbance, can also serve to greatly reduce forest complexity, by simplifying forest structure at stand or landscape scales, thus reducing resilience. The adaptive cycle (Figure 1) provides a conceptual model of ecosystem reorganisation and growth following disturbance. As an ecosystem moves through this cycle, it is more or less resilient at different phases. We will use this model to describe how the combined effects of MPB-caused disturbance and management can influence forest ecosystem resilience.

Lodgepole pine is a disturbance-adapted species that persists in landscapes despite repeated MPB outbreaks and wildfire [124]. Compared to stand-replacing disturbances (e.g., wildfire), MPB outbreaks are intermediate (generally 30%–50% mortality) disturbances that leave substantial secondary stand structure [14,54,124]; thus, under post MPB conditions, forest recovery proceeds relatively quickly. If beetle-impacted stands are managed by salvage logging then a significant alteration occurs in the backloop of the ecosystem reorganization phase ($\alpha$) of the adaptive cycle, potentially shifting the system to a less resilient state (pathway A in Figure 2). A combination of MPB attack and salvage logging diminishes the capacity for re-establishment of pre-disturbance communities, affects biogeochemical and hydrological processes, and develops a homogeneous landscape structure and composition [23,32,44,105]. In addition, salvage logging after MPB attack also negatively affects water quality, aquatic habitats and soil erosion [23,117,125–127]. Impairment of ecosystem recovery is one of the important ecological consequences of MPB-impacted salvage-logged forests. After disturbance, large ecological legacies can remain, which play crucial roles in ecosystem recovery and influence ecosystem processes for decades or centuries [128,129]. Salvage logging after disturbance (e.g., MPB attack) removes most of the biological legacies from the system, which leads to further damage of an already disturbed ecosystem [32]. The organisms in such a system may become maladapted due to interactive effects of two simultaneous disturbances (e.g., beetle attack and salvage logging) [32]. Moreover, salvage logging creates a homogeneous landscape structure and composition and a reduction in plant species richness and/or diversity [47–50]. As in most cases post logging (after timber harvest), stand recovery is facilitated through artificial regeneration with planting of nursery-grown tree seedlings. In the long run, such uniform landscapes are typically less resilient to disturbances and often experience more pest outbreaks than natural heterogeneous and complex forests [130–132]. In addition, any disturbance initiated in one part of a homogeneous landscape can easily be transmitted to other parts under favourable environmental conditions and can devastate the whole landscape [133,134]. Conversely, after natural disturbance, unsalvaged stands create a heterogeneous landscape structure with a mosaic of even-aged and uneven-aged patches [43,135]. These heterogeneous forests can recover faster than the salvage-logged stands as a significant portion of biological legacies (e.g., surviving trees, snags and logs, patches of intact vegetation, seedbanks in tree crowns or in the soil) of that particular ecosystem remain intact [136–138]. This allows the forest to remember its genetic, compositional and structural pre-harvest condition to build a new complex ecosystem [139], which, due to its increased heterogeneity, may be more adaptable to a changing climate and less susceptible to future disturbances [32,140]. Lastly, organisms are typically best adapted to the disturbance regimes under which they evolved [141,142]. Diverse and spatially heterogeneous natural systems are thus more resilient than homogeneous systems by providing support for all functional groups (pollinator, primary producers, herbivores etc.) and persistence of ecological function over time [143,144] (pathway B in Figure 2).

MPB-caused mortality increases diversity and complexity of the forests [46,54,55,60,107–109], which can be explained within the "intermediate disturbance hypothesis" whereby the highest species diversity can be achieved at intermediate rates and intensity of disturbance [145]. Under such conditions, ecosystems tend to have a mixture of pioneer and climax species [32], which makes the forest more diverse, complex and stable by including more pathways of energy flow [146]. In a recent study, Pec et al. [108] mentioned that understory community diversity and productivity increased across a gradient of increasing pine tree mortality. A similar observation was also reported by Stone and Wolfe [46] in northern Utah and Kovacic et al. [107] in eastern Colorado. In another study, Perovich and Sibold [60] reported that stands with MPB outbreak had greater diversity in age classes and species composition. In addition, natural disturbances generate tremendous amounts of dead wood, which can be used as habitats for many saproxylic (i.e., organisms that depend, during at least part of their life cycle, upon the dead or dying wood of moribund or dead trees, or upon other saproxylic organisms) species [147]. Based on a study by Müller et al. [148], European spruce bark beetle (*Ips typographus*) infestations improved the habitat of several endangered saproxylic beetles. In many cases, the presence or abundance of saproxylic species are used as bio-indicators of sustainable forest management [149,150] and positive indications of forest resilience. Dead wood can also significantly contribute to soil development by increasing soil fertility of poor sites [151]. In addition, removing dead trees by salvage logging is directly linked to soil drying and compaction, which alters the understory plant species composition, abundance and richness [47].

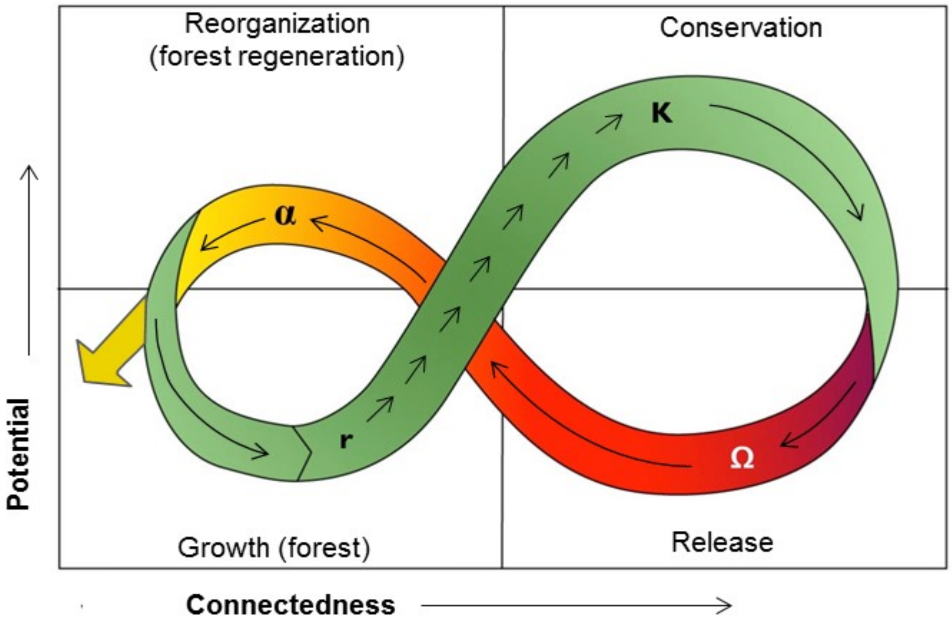


**Figure 1.** Adaptive cycle of a complex adaptive system. The arrows indicate the speed of change in the cycle: short, narrowly spaced arrows indicate slow change while long arrows indicate rapid change. The exit from the adaptive cycle at the left suggests where in the cycle the potential of the system can leak away and where a switch into a system with lower productivity and organization is most likely to occur. "**r**" denotes growth and exploitation of abundant resources, "**K**" denotes conservation, competitiveness, niche specialization for stabilization, "**Ω**" denotes release and new opportunities through disturbance, and "**α**" denotes recovery through reorganization (adapted from [121]).

The pathway that a forest ecosystem follows in the adaptive cycle after an MPB outbreak is thus highly dependent on the nature and intensity of management interventions. Too much salvage logging can lead to a system of greatly decreased resilience (Figure 2, pathway A) and thus increased susceptibility to future disturbances. Many authors have argued that this is one of the main reasons why the current MPB outbreak is in an epidemic stage in Canada [105]. Due to previous forest management policies, most of the MPB impacted Canadian pine forests were even-aged and homogenous in structure [22,43,44,152,153]. This relatively homogenous landscape, in conjunction with warming climates (warmer summer, mild winter), allowed the beetle population to spread exponentially. Present-day post-beetle forest management by salvage logging should thus seek to minimize such future disturbance events by, for example, planting a greater heterogeneity of species. Pathway B in Figure 2 represents an alternative and more resilient future forest. This forest is diverse, heterogeneous in spatial and vertical structure, maintains the memory of biological legacies, and supports a range of ecological processes that are connected across scales of space and time. Such a complex forest is more capable of system-level adaptation and re-organisation in response to future disturbances. Post-MPB outbreak management should seek to promote this complexity from the stand to the landscape scale.

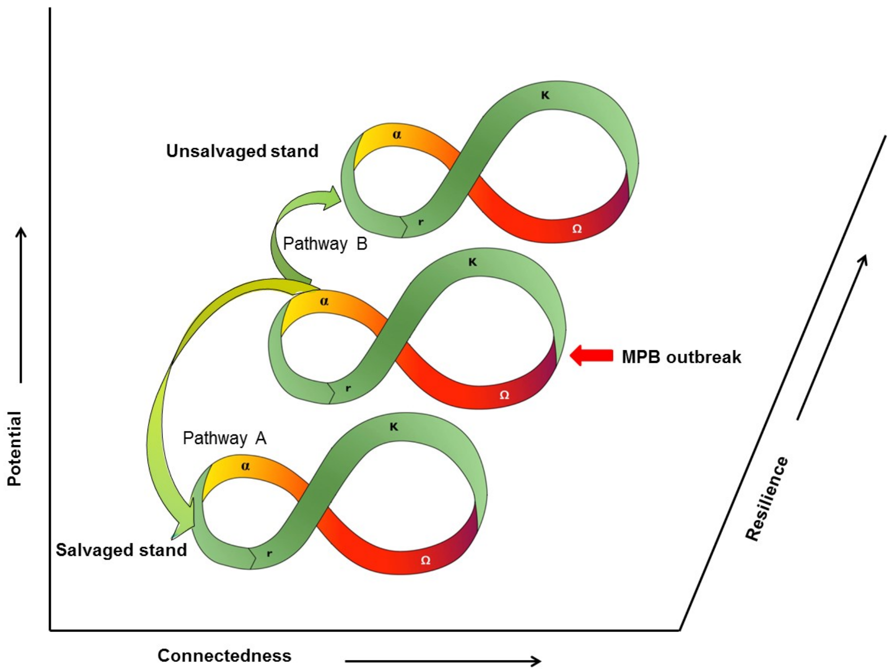


**Figure 2.** Adaptive cycles of MPB-impacted lodgepole pine forests through the lens of forest management policy. Less resilient forest stands can develop if salvage logging is used as a means of forest management (Pathway A), while more resilient forest stands can be developed in the absence of salvage logging (Pathway B).

## 10. Conclusions

The current MPB outbreak in BC crosses ecological, social and economic boundaries and its management goes beyond insect management. However, this literature review suggests that (i) a significant percent of residual secondary trees survived the beetle attack; (ii) stands in the current epidemic area appear to be recovering rapidly and in most cases can significantly contribute to mitigating the loss of mid-term timber supply; (iii) the occurrence of the MPB epidemic has resulted in more structurally and compositionally diverse forest stands; (iv) MPB-caused tree mortality may accelerate some tree species' geographic range expansion resulting from changing climatic conditions and (v) a comparatively small percentage of unsalvaged stands require management intervention for achieving mid-term timber supply goals. In addition, MPB-impacted, unsalvaged stands are likely to be more complex and heterogeneous in structure and, therefore, more ecologically resilient than stands developed following salvage logging. It is also critical that abundant numbers of live and dead standing trees be retained for wildlife habitat, and that forest understories are protected to allow rapid recovery and readjustment of the ecosystem [105]. Moreover, this new dimension of forest structure opens up the opportunity to design forests that are more diverse and more resilient to climate change, pest outbreaks and other unforeseen challenges that are sure to follow [123]. Post-beetle management should seek to reconcile social, ecological and economic objectives, retaining a patchwork of the best residual stands at the landscape scale, combined with salvage logging if necessary in stands where economic and ecological recovery objectives can best be met using this approach. However, ecological and economic impacts of the current mountain pine beetle outbreak need not be considered an unmitigated disaster. It is evident that lodgepole pine forests (at the stand and landscape level) in BC have experienced similar or even multiple outbreaks in the past and have naturally recovered over a short period of time [1,40]. We recommend the adoption of an ecosystem service-based, integrated forest management policy that seeks to maintain forest complexity and resilience from stand to landscape scales (see for example: [44,123,154]). Lastly, management decisions should be made using a combination of the best available data, local knowledge, professional judgment, and long term cost-benefit assessments that take into account the state of the future forest as well as the realization that MPB is an integral part of pine forest ecosystems in BC and most of its range.

**Acknowledgments:** This research was supported by a grant to Lael Parrott from the Natural Science and Engineering Research Council of Canada (grant No. NET GP 434810-12) to the TRIA Network, with contributions from Alberta Agriculture and Forestry, Foothills Research Institute, Manitoba Conservation and Water Stewardship, Natural Resources Canada—Canadian Forest Service, Northwest Territories Environment and Natural Resources, Ontario Ministry of Natural Resources and Forestry, Saskatchewan Ministry of Environment, West Fraser and Weyerhaeuser. We also thankful to two anonymous reviewers for their constructive suggestions that greatly improved the overall manuscript.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Axelson, J.; Alfaro, R.; Hawkes, B. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. *For. Ecol. Manag.* **2009**, *257*, 1874–1882. [CrossRef]
2. Alfaro, R.I.; Campbell, E.; Hawkes, B.C. *Historical Frequency, Intensity and Extent of Mountain Pine Beetle Disturbance in British Columbia*; MPB Working Paper 2009-30; Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre: Victoria, BC, Canada, 2010; p. 52.
3. Safranyik, L.; Carroll, A.L. The Biology and Epidemiology of the Mountain Pine Beetle in Lodgepole Pine Forests. *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine*; Safranyik, L., Wilson, B., Eds.; Natural Resources Canada: Victoria, BC, Canada, 2006; pp. 3–66.
4. Lee, S.; Kim, J.J.; Breuil, C. *Leptographium longiclavatum* sp. nov., a new species associated with the mountain pine beetle, *Dendroctonus ponderosae*. *Mycol. Res.* **2005**, *109*, 1162–1170. [CrossRef] [PubMed]
5. Lim, Y.W.; Kim, J.-J.; Lu, M.; Breuil, C. Determining fungal diversity on *Dendroctonus ponderosae* and *Ips pini* affecting lodgepole pine using cultural and molecular methods. *Fungal Divers.* **2005**, *19*, 79–94.
6. Rice, A.V.; Thormann, M.N.; Langor, D.L. Mountain pine beetle-associated blue-stain fungi are differentially adapted to boreal temperatures. *For. Path.* **2008**, *38*, 113–123. [CrossRef]
7. Whitney, H.; Spanier, O. An improved method for rearing axenic mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. Entomol.* **1982**, *114*, 1095–1100. [CrossRef]
8. Lieutier, F.; Yart, A.; Salle, A. Stimulation of tree defences by *Ophiostomatoid fungi* can explain attack success of bark beetles on conifers. *Ann. For. Sci.* **2009**, *66*, 801p1–801p22. [CrossRef]
9. Barras, S. Reduction of progeny and development in southern pine beetle following removal of symbiotic fungi. *Can. Entomol.* **1973**, *105*, 1295–1299. [CrossRef]
10. Ayres, M.; Wilkens, R.; Ruel, J.; Lombardero, M.; Vallery, E. Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi. *Ecology* **2000**, *81*, 2198–2210. [CrossRef]
11. Klepzig, K.; Moser, J.; Lombardero, M.; Ayres, M. Symbiosis and competition: Complex interactions among beetles, fungi and mites. *Symbiosis* **2001**, *30*, 93–96.
12. Bleiker, K.; Six, D. Dietary benefits of fungal associates to an eruptive herbivore: Potential implications of multiple associates on host population dynamics. *Environ. Entomol.* **2007**, *36*, 1384–1396. [CrossRef] [PubMed]

13. Amman, G.D.; McGregor, M.D.; Cahill, D.B.; Klein, W.H. *Guidelines for Reducing Losses of Lodgepole Pine to the Mountain Pine Beetle in Unmanaged Stands in The Rocky Mountains*; General Technical Report INT-36; USDA Forest Service: Ogden, Utah, UT, USA, 1977; p. 19.
14. Shore, L.T.; Safranyik, L.; Hawkes, C.B.; Taylor, W.S. Effects of the mountain pine beetle on lodgepole pine stand structure and dynamics. *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine*; Safranyik, L., Wilson, B., Eds.; Natural Resources Canada: Victoria, BC, Canada, 2006; pp. 95–116.
15. Price, T.S.; Doggett, C.; Pye, J.M.; Smith, B. *A History of Southern Pine Beetle Outbreaks in the Southeastern United States*; Georgia Forestry Commission: Atlanta, GA, USA, 1992; p. 65.
16. Safranyik, L.; Linton, D.A. Unseasonably low fall and winter temperatures affecting mountain pine beetle and pine engraver beetle populations and damage in the British Columbia Chilcotin Region. *J. Entomol. Soc. B.C.* **1991**, *88*, 17–21.
17. Safranyik, L. Mountain pine beetle epidemiology in lodgepole pine. In Proceedings of the Stone Mountain Pine Beetle Symposium: Challenges and Solutions, Victoria, BC, Canada, 30–31 October 2003; Shore, T.L., Brooks, J.E., Eds.; Information Report BC-X-399. Natural Resources Canada, Pacific Forestry Centre: Victoria, BC, Canada, 2004; p. 298.
18. Alfaro, R.I.; Campbell, R.; Vera, P.; Hawkes, B.; Shore, T. Dendroecological reconstruction of mountain pine beetle outbreaks in the Chilcotin Plateau of British Columbia. In Proceedings of the Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, BC, Canada, 30–31 October 2003; Shore, T.L., Brooks, J.E., Stone, J.E., Eds.; Information Report BC-X-399; Resources Canada, Canadian, Forest Service, Pacific Forestry Centre: Victoria, BC, Canada, 2004; pp. 245–256.
19. Taylor, S.W.; Carroll, A.L.; Alfaro, R.I.; Safranyik, L. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine*; Safranyik, L., Wilson, W.R., Eds.; Canadian Forest Service: Victoria, BC, Canada, 2006; pp. 67–94.
20. Cole, W.E.; Amman, G.D. *Mountain Pine Beetle Dynamics in Lodgepole Pine Forests, Part 1: Course of An Infestation*; General Technical Report INT-89; U.S. Department of Agriculture Forest Service, Intermountain Research Station: Ogden, UT, USA, 1980; p. 64.
21. McIntosh, A.C.S.; Macdonald, S.E. Potential for lodgepole pine regeneration after mountain pine beetle attack in newly invaded Alberta stands. *For. Ecol. Manag.* **2013**, *295*, 11–19. [CrossRef]
22. Walton, A. *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: Victoria, BC, Canada, 2013. Available online: http://www.for.gov.bc.ca/ftp/hre/external/!publish/web/bcmpb/year10/BCMPB.v10.BeetleProjection.Update.pdf (accessed on 3 December 2015).
23. Dhar, A.; Balliet, N.A.; Runzer, K.D; Hawkins, C.D.B. Impact of a mountain pine beetle outbreak on young lodgepole pine stands in central British Columbia. *Forests* **2015**, *6*, 3483–3500. [CrossRef]
24. Association of BC Forest Professional (ABCFP). *Mid-Term Timber Supply Advocacy Report*; Association of BC Forest Professionals: Victoia, BC, Canada, 2011. Available online: http://www.abcfp.ca/publications_forms/publications/documents/Mid-term_TimberSupply_ABCFP_Summary_Report.pdf (accessed on 22 October 2015).
25. Dhar, A.; Parrott, L.; Heckbert, S. Mapping the impact of mountain pine beetle outbreaks on forest ecosystem services in British Columbia, Canada. In Proceedings of the IUFRO Landscape Ecology Conference Sustaining Ecosystem Services in Forest Landscapes Concepts, Research, and Applications, Tartu, Estonia, 23–30 August 2015. Available online: http://iufrole2015.to.ee/download/m55d4ea9be5748#iufrole_2015_abstracts_pdf (accessed on 22 February 2016).
26. Coops, N.C.; Timko, J.A.; Wulder, M.A.; White, J.C.; Ortlepp, S.M. Investigating the effectiveness of Mountain Pine Beetle mitigation strategies. *Int. J. Pest Manag.* **2008**, *54*, 151–165. [CrossRef]
27. Fettig, C.J.; Gibson, K.E.; Munson, A.S.; Negrón, J.F. Cultural practices for prevention and mitigation of mountain pine beetle infestations. *For. Sci.* **2014**, *60*, 450–463.
28. Gillette, N.E.; Wood, D.L.; Hines, S.J.; Runyon, J.B.; Negrón, J.F. Consequences of mountain pine beetle treatment decisions. *For. Sci.* **2014**, *60*, 527–538.

29. Fettig, C.J.; Munson, A.S.; Grosman, D.M.; Bush, P.B. Evaluations of emamectin benzoate and propiconazole for protecting individual *Pinus contorta* from mortality attributed to colonization by *Dendroctonus ponderosae* and associated fungi. *Pest. Manag. Sci.* **2013**, *70*, 771–778. [CrossRef] [PubMed]
30. Progar, R.A.; Gillette, N.E.; Fettig, C.J.; Hrinkevich, K.H. Applied chemical ecology of the mountain pine beetle. *For. Sci.* **2014**, *60*, 414–433.
31. Eng, M.A. *Forest Stewardship in the Context of Large-Scale Salvage Operations: An Interpretation Paper*; Technical Report 019; British Columbia Ministry of Forests, Forest Science Program: Victoria, BC, Canada, 2004. Available online: https://www.for.gov.bc.ca/hfd/pubs/docs/tr/tr019.pdf (accessed on 22 January 2016).
32. Lindenmayer, D.B.; Burton, P.J.; Franklin, F.J. *Salvage Logging and its Ecological Consequences*; Island Press: Washington, DC, USA, 2008; p. 246.
33. Six, L.D.; Biber, E.; Long, E. Management for Mountain Pine Beetle Outbreak Suppression: Does Relevant Science Support Current Policy? *Forests* **2014**, *5*, 103–133. [CrossRef]
34. Schoennagel, T.; Veblen, T.T.; Negron, J.F.; Smith, J.M. Effects of Mountain Pine Beetle on Fuels and Expected Fire Behavior in Lodgepole Pine Forests, Colorado, USA. *PLoS ONE* **2012**, *7*, e30002. [CrossRef] [PubMed]
35. Harveya, B.J.; Donatob, D.C.; Turnera, M.G. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. *Proc. Natl. Acad. Sci.* **2014**, *111*, 15120–15125. [CrossRef] [PubMed]
36. Hart, S.J.; Schoennagela, T.; Veblena, T.T.; Chapmana, T.B. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proc. Natl. Acad. Sci.* **2015**, *111*, 4375–4380. [CrossRef] [PubMed]
37. Roe, A.L.; Amman, G.D. *The Mountain Pine Beetle in Lodgepole Pine Forests*; Research Paper INT-71; US Department of Agriculture Forest Service, Intermountain Research Station: Ogden, UT, USA, 1970; p. 28.
38. Stuart, J.D.; Agee, J.K.; Gara, R.I. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. *Can. J. For. Res.* **1989**, *19*, 1096–1104. [CrossRef]
39. Heath, R.; Alfaro, R. Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle: A case study. *J. Entomol. Soc. B.C.* **1990**, *87*, 16–21.
40. Hawkes, B.; Taylor, S.W.; Stockdale, C.; Shore, T.L.; Alfaro, R.I.; Campbell, R.; Vera, P. Impact of mountain pine beetle on stand dynamics in British Columbia. In Proceedings of the Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, BC, Canada, 30–31 October 2003; Shore, T.L., Brooks, J.E., Stone, J.E., Eds.; Information Report BC-X-399. Natural Resources Canada, Canadian, Forest Service, Pacific Forestry Centre: Victoria, BC, Canada, 2004; pp. 177–199.
41. Berg, E.E.; Henry, J.D.; Fastie, C.L.; Volder, A.D.; Matsuoka, S.M. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *For. Ecol. Manag.* **2006**, *227*, 219–232. [CrossRef]
42. Hawkins, C.D.B.; Dhar, A.; Balliet, N. Radial growth of residual overstory trees and understory saplings after mountain pine beetle attack in central British Columbia. *For. Ecol. Manag.* **2013**, *310*, 348–356. [CrossRef]
43. Dhar, A.; Hawkins, C.D.B. Regeneration and growth following mountain pine beetle attack: A synthesis of knowledge. *J. Ecosyst. Manag.* **2011**, *12*, 1–16.
44. Dhar, A.; Parrott, L.; Heckbert, S. Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada. *Can. J. For. Res.* **2016**, *46*, 987–999. [CrossRef]
45. British Columbia Ministry of Forests and Range. *Forests for Tomorrow: Planning, Reforestation and Brushing Focused in Catastrophic Event-Impacted Management Units*; Forest Practices Branch: Victoria, BC, Canada, 2005; p. 27.
46. Stone, W.E.; Wolfe, M.L. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio* **1996**, *122*, 1–12. [CrossRef]
47. Purdon, M.; Brais, S.; Bergeron, Y. Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. *Appl. Veg. Sci.* **2004**, *7*, 49–60. [CrossRef]
48. Marzano, R.; Garbarino, M.; Marcolin, E.; Pividori, M.; Lingua, E. Deadwood anisotropic facilitation on seedling establishment after a stand-replacing wildfire in Aosta Valley (NW Italy). *Ecol. Eng.* **2013**, *51*, 117–122. [CrossRef]

49. Kurulok, S.E.; Macdonald, S.E. Impacts of post fire salvage logging on understory plant communities of the boreal mixedwood forest 2 and 34 years after disturbance. *Can. J. For. Res.* **2007**, *37*, 2637–2651. [CrossRef]
50. D'Amato, A.W.; Fraver, S.; Palik, B.J.; Bradford, J.B.; Patty, L. Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *For. Ecol. Manag.* **2011**, *262*, 2070–2078. [CrossRef]
51. Coates, K.D.; DeLong, C.; Burton, P.J.; Sachs, D.L. *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, BC, Canada, 2006; p. 17.
52. Coates, K.D.; Glover, T.; Henderson, B. *Abundance of Secondary Structure in Lodgepole Pine Stands Affected by the Mountain Pine Beetle in the Cariboo-Chilcotin*; Mountain Pine Beetle Working Paper; Canadian Forest Service, Pacific Forestry Centre: Victoria, BC, Canada, 2009. Available online: http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/31195.pdf (accessed on 7 April 2016).
53. Vyse, A.; Ferguson, C.; Huggard, D.J.; Roach, J.; Zimonick, B. Regeneration beneath lodgepole pine dominated stands attacked or threatened by the mountain pine beetle in the south central Interior, British Columbia. *For. Ecol. Manag.* **2006**, *258*, S36–S43. [CrossRef]
54. Hawkins, C.D.B.; Dhar, A.; Balliet, N.A.; Runzer, K.D. Residual mature trees and secondary stand structure after mountain pine beetle attack in central British Columbia. *For. Ecol. Manag.* **2012**, *277*, 107–115. [CrossRef]
55. Amoroso, M.M.; Coates, K.D.; Astrup, R. Stand recovery and self-organization following large-scale mountain pine beetle induced canopy mortality in northern forests. *For. Ecol. Manag.* **2013**, *310*, 300–311. [CrossRef]
56. DeLong, C.; Rogers, B.; Kaytor, B. Response of understory trees to MPB attack in permanent sample plots three years after establishment in the Sub-Boreal Spruce zone. In Proceedings of the Growth and Yield Modelling Workshop "Regeneration and Growth Following MPB Attack: A synthesis of Knowledge", University of Northern British Columbia, Prince George, BC, Canada, 23–24 September 2008; Forsythe, P., Hawkins, C., Hassegawa, M., Eds.; University of Northern British Columbia: Prince George, BC, Canada, 2009; pp. 6–7.
57. Statland, C.B. Advanced regeneration in pine thinning trials killed by mountain pine beetle. In Proceedings of the Growth and Yield Modelling Workshop "Regeneration and Growth Following MPB Attack: A synthesis of Knowledge", University of Northern British Columbia, Prince George, BC, Canada, 23–24 September 2008; Forsythe, P., Hawkins, C., Hassegawa, M., Eds.; University of Northern British Columbia: Prince George, BC, Canada, 2009; pp. 4–5.
58. Zumrawi, A.; Sattler, D.; LeMay, V.; Marshall, P.; Lee, T. Predicting natural regeneration within the Prognosis BC framework following MPB attack: Imputation and hybrid modeling. In Proceedings of the Growth and Yield Modelling Workshop "Regeneration and Growth Following MPB Attack: A synthesis of Knowledge", University of Northern British Columbia, Prince George, BC, Canada, 23–24 September 2008; Forsythe, P., Hawkins, C., Hassegawa, M., Eds.; University of Northern British Columbia: Prince George, BC, Canada, 2009; pp. 8–10.
59. Astrup, R.; Coates, D.K.; Hall, E. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. *For. Ecol. Manag.* **2008**, *256*, 1743–1750. [CrossRef]
60. Perovich, P.; Sibold, J.S. Forest composition change after a mountain pine beetle outbreak, Rocky Mountain National Park, CO, USA. *For. Ecol. Manag.* **2016**, *366*, 184–192. [CrossRef]
61. Nigh, G.D.; Antos, J.A.; Parish, R. Density and distribution of advance regeneration in mountain pine beetle killed lodgepole pine stands of the Montane Spruce zone of southern British Columbia. *Can. J. For. Res.* **2008**, *38*, 2826–2836. [CrossRef]
62. Griesbauer, H.; Green, S. Examining the utility of advance regeneration for reforestation and timber production in unsalvaged stands killed by the mountain pine beetle: Controlling factors and management implications. *J. Ecosyst. Manag.* **2006**, *7*, 81–92.
63. Dale, V.H.; Lugo, A.E.; MacMahon, J.A.; Pickett, S.T.A. Ecosystem management in the context of large infrequent disturbances. *Ecosystems* **1998**, *1*, 546–557. [CrossRef]
64. Waring, R.H.; Pitman, G.B. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* **1985**, *66*, 889–897. [CrossRef]
65. Murphy, T.E.L.; Adams, D.L.; Ferguson, D.E. Response of advance lodgepole pine regeneration to overstory removal in eastern Idaho. *For. Ecol. Manag.* **1999**, *120*, 234–244.

66. Romme, W.H.; Knight, D.H.; Fedders, J. Mountain pine beetle outbreaks in the Rocky Mountains: Effects on fuels and fire in lodgepole pine forest (abstract). In *Program of the Annual Meeting of the Ecological Society of America*; Syracuse University: Syracuse, NY, USA, 1986; p. 290.
67. Dhar, A.; Coates, K.D.; Rogers, B.; Hardy, K. Impact of Mountain pine beetle on mid-term timber supply in sub boreal spruce zone of British Columbia. In *16th International Boreal Forest Research Association (IBFRA) Conference*; Comeau, P., Ed.; IBRF: Edmonton, AB, Canada, 2013; p. 28.
68. Kimmins, J.P. *Forest Ecology*; Macmillan Publishing Company: New York, NY, USA, 1987; p. 531.
69. Smith, F.W.; Resh, S.C. Age-related changes in production and below-ground carbon allocation in Pinus contorta forests. *For. Sci.* **1999**, *45*, 333–341.
70. Kashian, D.M.; Romme, W.H.; Tinker, D.B.; Turner, M.G.; Ryan, M.G. Post-fire changes in forest carbon storage over a 300-year chronosequence of *Pinus contorta*-dominated forests. *Ecol. Monogr.* **2013**, *83*, 49–66. [CrossRef]
71. Bogdanski, B.; Sun, L.; Peter, B.; Stennes, B. *Markets for Forest Products Following A Large Disturbance: Opportunities and Challenges from the Mountain Pine Beetle Outbreak in Western Canada*; Report BC-X-429; Canada Forest Services: Victoria, BC, Canada, 2011. Available online: http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/32226.pdf (accessed on 16 February 2015).
72. BC Ministry of Forests and Range. *Timber Supply and the Mountain Pine Beetle Infestation in British Columbia: 2007 Update*; Forest Analysis and Inventory Branch, BC Ministry of Forests and Range: Victoria, BC, Canada, 2007; p. 32.
73. Pousette, J.; Hawkins, C. An assessment of critical assumptions supporting the timber supply modelling for mountain-pine-beetle-induced allowable annual cut uplift in the Prince George Timber Supply Area. *J. Ecosyst. Manag.* **2006**, *7*, 93–104.
74. Patriquin, M.N.; Wellstead, A.M.; White, W.A. 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.* **2007**, *9*, 938–946. [CrossRef]
75. Coates, K.D. *Evaluation of Stand Dynamics after A 25–30 Year Old Mpb Attack in the Flathead Region of South Eastern British Columbia*; FIA-FSP project # M085196; Bulkley Valley Research Centre: Smithers, BC, Canada, 2008. Available online: http://www.for.gov.bc.ca/hfd/library/FIA/2008/FSP_M085196.pdf (accessed on 12 October 2015).
76. Coates, K.D.; Hall, E.C. *Implications of Alternative Silvicultural Strategies in Mountain Pine Beetle Damaged Stands*; Technical Report for Forest Science Project Y051161; Bulkley Valley Centre for Natural Resources Research and Management: Smithers, BC, Canada, 2005; p. 23.
77. Runzer, K.; Hassegawa, M.; Balliet, N.; Bittencourt, E.; Hawkins, C.D.B. *Temporal Composition and Structure of Post-Beetle Lodgepole Pine Stands: Regeneration, Growth, Economics, and Harvest Implications*; Mountain Pine Beetle Initiative Working Paper 2008-23; Canadian Forest Service: Victoria, BC, Canada, 2008; p. 76.
78. Pousette, J. Secondary Stand Structure and Its Timber Supply Implication for Mountain Pine Beetle Attacked Forests on the Nechako Plateau of British Columbia. Master's Thesis, University of Northern British Columbia, Prince George, BC, Canada, 2010. p. 182.
79. Lynch, H.J.; Renkin, R.A.; Crabtree, R.L.; Moorcroft, P.R. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems* **2006**, *9*, 1318–1327. [CrossRef]
80. Jenkins, M.J.; Hebertson, E.; Page, W.; Jorgenson, C.A. Bark beetles, fuels, fires and implications for forest management in the intermountain west. *For. Ecol. Manag.* **2008**, *254*, 16–34. [CrossRef]
81. Hicke, J.A.; Johnson, M.C.; Hayes, J.L.; Preisler, H.K. Effects of bark beetle-caused tree mortality on wildfire. *For. Ecol. Manag.* **2012**, *271*, 81–90. [CrossRef]
82. Jenkins, M.J.; Runyon, J.B.; Fettig, C.J.; Page, W.G.; Bentz, B.J. Interactions among the mountain pine beetle, fires, and fuels. *For. Sci.* **2014**, *60*, 489–501. [CrossRef]
83. Jolly, W.M.; Parsonsa, R.A.; Hadlowa, A.M.; Cohna, G.M.; McAllister, S.S.; Popp, J.B.; Hubbard, R.M.; Negron, J.F. Relationships between moisture, chemistry, and ignition of Pinus contorta needles during the early stages of mountain pine beetle attack. *For. Ecol. Manag.* **2012**, *269*, 52–59. [CrossRef]
84. Page, W.G.; Jenkins, M.J.; Runyon, J.B. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Can. J. Res.* **2012**, *42*, 1631–1647. [CrossRef]

85. Collins, B.J.; Rhoades, C.C.; Battaglia, M.A.; Hubbard, R.M. 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. Manag.* **2012**, *284*, 260–268. [CrossRef]
86. Simard, M.; Romme, W.; Griffin, J. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecol. Monogr.* **2011**, *81*, 3–24. [CrossRef]
87. Klutsch, G.J.; Battaglia, M.A.; West, D.R.; Costello, S.L.; Negrón, J.F. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. *West J. Appl. For.* **2011**, *26*, 201–109.
88. Bourbonnais, M.L.; Nelson, T.A.; Wulder, M.A. Geographic analysis of the impacts of mountain pine beetle infestation on forest fire ignition. *Can. Geogr.* **2014**, *58*, 188–202. [CrossRef]
89. Meigs, G.W.; Campbell, J.L.; Zald, H.S.; Bailey, J.D.; Shaw, D.C.; Kennedy, R.E. Does wildfire likelihood increase following insect outbreaks in conifer forests? *Ecosphere* **2015**, *6*. [CrossRef]
90. Kulakowski, D.; Jarvis, D. 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. Manag.* **2011**, *262*, 1686–1696. [CrossRef]
91. Mattson, W.J.; Addy, N.D. Photophagous insect as regulators of forest primary production. *Science* **1975**, *190*, 515–522. [CrossRef]
92. Loreau, M. Consumers as maximizers of matter and energy flow in ecosystems. *Am. Nat.* **1995**, *145*, 22–42. [CrossRef]
93. 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.; et al. Global Consequences of Land Use. *Science* **2005**, *309*, 570–574. [CrossRef] [PubMed]
94. Kurz, W.A.; Dymond, C.C.; Stinson, G.; Rampley, G.J.; Neilson, E.T.; Carroll, A.L.; Ebata, T.; Safranyik, L. Mountain pine beetle and forest carbon feedback to climate change. *Nature* **2008**, *452*, 987–990. [CrossRef] [PubMed]
95. Caldwell, M.K. Impacts of Mountain Pine Beetle (*Dendroctonus Ponderosae*) and Fire Disturbances on Forest Ecosystem Carbon Dynamics and Species Composition. Master's Thesis, University of Colorado, Denver, CO, USA, 2012; p. 95.
96. Mathys, A.; Black, T.A.; Nesic, Z.; Nishio, G. Carbon balance of a partially-harvested mixed conifer forest following mountain pine beetle attack and its comparison to a clearcut. *Biogeosciences* **2013**, *10*, 5451–5463. [CrossRef]
97. Reed, E.D.; Ewers, E.B.; Pendall, E. Impact of mountain pine beetle induced mortality on forest carbon and water fluxes. *Environ. Res. Lett.* **2014**, *9*, 105004. [CrossRef]
98. Emmel, C.; Paul-Limgoes, E.; Bowler, R.; Black, T.A.; Christen, A. Vertical distribution of Carbon dioxide sources and sinksin a recovering mountain pine beetle-attack lodgepole pine stand. *Agric. For. Meteorol.* **2014**, *195*, 108–122. [CrossRef]
99. Fettig, C.J.; Reid, M.L.; Bentz, B.J.; Sevanto, S.; Spittlehouse, D.L.; Wang, T. Changing climates, changing forests: A western North American perspective. *J. For.* **2013**, *111*, 214–228. [CrossRef]
100. Hansen, E.M.; Amacher, C.M.; Miegroet, H.V.; Long, J.; Ryan, M.G. Carbon Dynamics in Central US Rockies Lodgepole Pine Type After Mountain Pine Beetle Outbreaks. *For. Sci.* **2015**, *61*, 665–679.
101. Amiro, B.D.; Barr, A.G.; Barr, J.G.; Black, T.A.; Bracho, R.; Brown, M.; Chen, J.; Clark, K.L.; Davis, K.J.; Desai, A.R.; et al. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J. Geophys. Res.* **2010**, *115*. [CrossRef]
102. Brown, M.; Black, T.A.; Nesic, Z.; Foordb, V.N.; Spittlehousec, D.L.; Fredeen, A.L.; Grant, N.J.; Burton, P.J.; Trofymow, J.A. Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia. *Agric. For. Meteorol.* **2010**, *150*, 254–264. [CrossRef]
103. Arora, V.K.; Peng, Y.; Kurz, W.A.; Fyfe, J.C.; Hawkins, B.; Werner, A.T. Potential near-future carbon uptake overcomes losses from a large insect outbreak in British Columbia, Canada. *Geophys. Res. Lett.* **2016**, *43*. [CrossRef]
104. Hamann, A.; Wang, T.L. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* **2006**, *87*, 2773–2786. [CrossRef]
105. Burton, P.J. Striving for sustainability and resilience in the face of unprecedented change: The case of the mountain pine beetle outbreak in British Columbia. *Sustainability* **2010**, *2*, 2403–2423. [CrossRef]

106. Von Holle, B.; Delcourt, H.R.; Simberloff, D. The importance of biological inertia in plant community resistance to invasion. *J. Veg. Sci.* **2003**, *14*, 425–432. [CrossRef]
107. Kovacic, D.A.; Dyer, M.I.; Cringan, A.T. Understory biomass in ponderosa pine following mountain pine beetle infestation. *For. Ecol. Manag.* **1985**, *13*, 53–67. [CrossRef]
108. Pec, G.J.; Karst, J.; Sywenky, A.N.; Cigan, P.W.; Erbilgin, N.; Simard, S.W.; Cahill, J.F., Jr. Rapid Increases in Forest Understory Diversity and Productivity following a Mountain Pine Beetle (*Dendroctonus ponderosae*) Outbreak in Pine Forests. *PLoS ONE* **2015**, *10*, e0124691. [CrossRef] [PubMed]
109. Edwards, M.; Krawchuk, M.M.; Burton, P.J. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. *For. Ecol. Manag.* **2015**, *335*, 163–175. [CrossRef]
110. Chan-McLeod, A.C.A. A review and synthesis of the effects of unsalvaged mountain-pine-beetle-attacked stands on wildlife and implications for forest management. *J. Ecosyst. Manag.* **2006**, *7*, 119–132.
111. Martin, K.; Norris, A.; Drever, M. Effects of bark beetle outbreaks on avian biodiversity in the British Columbia interior: Implications for critical habitat management. *J. Ecosyst. Manag.* **2006**, *7*, 10–24.
112. Saab, V.A.; Latif, Q.S.; Rowland, M.M.; Johnson, T.N.; Chalfoun, A.D.; Buskirk, S.W.; Heyward, J.E.; Dresser, M.A. Ecological Consequences of Mountain Pine Beetle Outbreaks for Wildlife in Western North American Forests. *For. Sci.* **2014**, *60*, 539–559.
113. Stone, W.E. The Impact of A Mountain Pine Beetle Epidemic on Wildlife Habitat and Communities in Post Epidemic Stands of Lodgepole Pine Forests in Northern Utah. Ph.D. Thesis, Utah S University, Logan, UT, USA, 1995. p. 229.
114. Drever, M.C.; Aitken, K.E.H.; Norris, A.R.; Martin, K. Woodpeckers as reliable indicators of bird richness, forest health and harvest. *Biol. Conserv.* **2008**, *141*, 624–634. [CrossRef]
115. Walters, E.L.; Miller, E.H.; Lowther, P.E. *Red-Breasted Sapsucker (Sphyrapicus Ruber) and Red-Naped Sapsucker (Sphyrapicus Nuchalis)*; Poole, A., Gill, F., Eds.; The Birds of North America: Philadelphia, PA, USA, 2002. Available online: http://www.ericlwalters.ca/rnsarbsaBNA.pdf (accessed on 5 July 2016).
116. Bonnot, T.W.; Rumble, M.A.; Millspaugh, J.J. Nest success of black-backed woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. *Condor* **2008**, *110*, 450–457. [CrossRef]
117. Bunnell, F.L.; Kremsater, L.L.; Houde, I. *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, BC, Canada, 2011; p. 99.
118. Ferrari, M.R.; Miller, J.R.; Russell, G.L. Modeling changes in summer temperature of the Fraser River during the next century. *J. Hydrol.* **2007**, *342*, 336–346. [CrossRef]
119. Johannes, M.R.S.; Kenney, A.; Pouliotte, J.; Steele, D. Mountain Pine Beetle Threats to Salmon and Fisheries Resources. In Proceedings of the Pacific Salmon Foundation and Fraser Basin Council Workshop, Prince George, BC, Canada, 30–31 January 2007; p. 71.
120. Wong, C. *Environmental Impacts of Mountain Pine Beetle in the Southern Interior*; British Columbia Ministry of Environment: Prince George, BC, Canada, 2008. Available online: http://www.sibacs.com/wp-content/uploads/2009/02/environmental-impacts-report-final.pdf (accessed on 16 July 2016).
121. Gunderson, L.H.; Holling, C.S. *Panarchy: Understanding Transformations in Human and Natural Systems*; Island Press: Washington, DC, USA, 2002; p. 507.
122. Parrott, L.; Meyer, W.S.W. Future landscapes: Managing within complexity. *Front. Ecol. Environ.* **2012**, *10*, 382–389. [CrossRef]
123. Messier, C.; Puettmann, K.; Chazdon, R.; Andersson, K.P.; Angers, V.A.; Brotons, L.; Filotas, E.; Tittler, R.; Parrott, L.; Levin, S.A. From Management to Stewardship: Viewing Forests as Complex Adaptive Systems in an Uncertain World. *Conserv. Lett.* **2015**, *8*, 368–377. [CrossRef]
124. Hansen, E.M. Forest development and carbon dynamics after mountain pine beetle outbreaks. *For. Sci.* **2014**, *60*, 476–488.
125. Bunnell, F.; Squires, K.A.; Houde, I. *Evaluating Effects of Large-Scale Salvage Logging for Mountain Pine Beetle in Terrestrial and Aquatic Vertebrates*; Natural Resources Canada: Victoria, BC, Canada, 2004; p. 57.
126. Brown, S.; Schreier, H. *Water quantity and quality related to rates of pine beetle infestation and salvage logging: A regional comparison*; Water quality technical report, MPB Project #7.31; University of British Columbia: Vancouver, BC, Canada, 2009; p. 24.

127. Mikkelson, K.; Bearup, L.A.; Maxwell, R.M.; Stednick, J.D.; McCray, J.E.; Sharp, J.O. Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects. *Biogeochemistry* **2013**, *115*, 1–21. [CrossRef]
128. Foster, D.R.; Knight, D.H.; Franklin, J.F. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* **1998**, *1*, 497–510. [CrossRef]
129. Turner, M.G.; Dale, V.H. Comparing large, infrequent disturbances: What have we learned? *Ecosystems* **1998**, *1*, 493–496. [CrossRef]
130. Schowalter, T.D. Forest pest management: A synopsis. *Northwest Environ. J.* **1988**, *4*, 313–318.
131. Perry, D.A. The scientific basis of forestry. *Annu. Rev. Ecol. Syst.* **1998**, *29*, 435–466. [CrossRef]
132. Coyle, D.R.; Nebeker, T.E.; Hart, E.R.; Mattson, W.J. Biology and management of insect pets in North American intensively managed hardwood forest systems. *Annu. Rev. Entomol.* **2005**, *50*, 1–29. [CrossRef] [PubMed]
133. Turner, M.G.; Romme, W.H. Landscape dynamics in crown fire ecosystems. *Landsc. Ecol.* **1994**, *9*, 59–77. [CrossRef]
134. Bergeron, Y.; Richard, P.J.H.; Carcaillet, C.; Gauthier, S.; Flannigan, M.; Prairie, Y.T. Variability in the Fire Frequency and Forest Composition in Canada's Southeastern Boreal Forest: A Challenge For Sustainable Forest Management. Available online: http://www.consecol.org/vol2/iss2/art6/ (accessed on 12 November 2015).
135. Agee, J.K. *Fire Ecology of Pacific Northwest Forests*; Island Press: Washington, DC, USA, 1993; p. 505.
136. Gustafsson, L.; Baker, S.C.; Bauhus, J.; Beese, W.J.; Brodie, A.; Kouki, J.; Lindenmayer, D.B.; Lõhmus, A.; Pastur, G.M.; Messier, C.; et al. Retention forestry to maintain multifunctional forests: A world perspective. *BioScience* **2012**, *62*, 633–645.
137. Lindenmayer, D.B.; Franklin, J.F.; Lõhmus, A.; Bake, S.C.; Bauhus, J.; Beese, W.; Brodie, A.; Kiehl, B.; Kouki, J.; Pastur, G.M.; et al. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conserv. Lett.* **2012**, *5*, 421–431. [CrossRef]
138. Fedrowitz, K.; Koricheva, J.; Bake, R S.C.; Lindenmayer, D.B.; Palik, B.; Rosenvald, R.; Beese, W.; Franklin, J.F.; Kouki, J.; Macdonald, E.; et al. Can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl. Ecol.* **2014**, *51*, 1669–1679. [CrossRef] [PubMed]
139. Drever, R.C.; Peterson, G.; Messier, C.; Bergeron, Y.; Flannigan, M. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.* **2006**, *36*, 2285–2299. [CrossRef]
140. Park, A.; Puettmann, K.; Wilson, E.; Messier, C.; Kames, S.; Dhar, A. Can boreal and temperate forest management be adapted to the uncertainties of 21st century climate change? *Crit. Rev. Plant Sci.* **2014**, *33*, 251–285. [CrossRef]
141. Bunnell, F. Forest-dwelling fauna and natural fire regimes in British Columbia: Patterns and implications for conservation. *Conserv. Biol.* **1995**, *9*, 636–644. [CrossRef]
142. Covington, W.W. The evolutionary and history context. In *Ecological Restoration of Southwestern Ponderosa Pine Forests*; Friedrici, P., Ed.; Island press: Washington, DC, USA, 2003; pp. 26–47.
143. Schneider, D.W. Experimental perturbation of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* **1990**, *57*, 25–41.
144. McCann, K.S. The diversity-stability debate. *Nature* **2000**, *405*, 228–233. [CrossRef] [PubMed]
145. Connell, J.H. Diversity in tropical rain forests and coral reefs. *Science* **1978**, *199*, 1302–1310. [CrossRef] [PubMed]
146. Hooper, D.U.; Chapin, F.S.; Ewel, J.J.; Hector, A.; Inchausti, P.; Lavorel, S.; Lawton, J.H.; Lodge, D.M.; Loreau, M.; Naeem, S.; et al. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* **2005**, *75*, 3–35. [CrossRef]
147. Lindhe, A.; Lindelöw, Å.; Åsenblad, N. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodivers. Conserv.* **2005**, *14*, 3033–3053. [CrossRef]
148. Müller, J.; Noss, R.F.; Bussler, H.; Brandl, R. Learning from a "benign neglect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation. *Biol. Conserv.* **2010**, *143*, 2559–2569. [CrossRef]
149. Lindenmayer, D.B. Future directions for biodiversity conservation in managed forests: Indicator species, impact studies and monitoring programs. *For. Ecol. Manag.* **1999**, *115*, 277–287. [CrossRef]
150. Arignan, V.; Villard, M.A. Selecting indicator species to monitor ecological integrity: A review. *Environ. Monit. Assess.* **2002**, *78*, 45–61. [CrossRef]

151. Duncan, R.P. Flood disturbance and coexistence of species in a lowland podocarp forest, south Westland, New Zealand. *J. Ecol.* **1993**, *81*, 403–416. [CrossRef]
152. Taylor, S.; Carroll, A. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. In Proceedings of the Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, BC, Canada, 30–31 October 2003; Shore, T.L., Brooks, J.E., Stone, J.E., Eds.; Information Report BC-X-399; Natural Resources Canada, Canadian, Forest Service, Pacific Forestry Centre: Victoria, BC, Canada, 2004; pp. 41–51.
153. Dhar, A.; Parrott, L. Salvage logging after mountain pine beetle outbreaks reduces the social-ecological resilience of forest landscapes. In Proceedings of the Mountain Pine Beetle Information Exchange Forum, Edmonton, Alberta, AB, Canada, 22–23 April 2015; McClain, K., Ed.; Foothill Research Center: Hinton, AB, Canada, 2015; p. 17.
154. Messier, C.; Puettmann, K.J.; Coates, K.D. *Managing Forests as Complex Adaptive Systems: Building Resilience to the Challenge of Global Change*; Routledge: New York, NY, USA, 2013; p. 368.