Review

Spruce Beetle Biology, Ecology and Management in the Rocky Mountains: An Addendum to Spruce Beetle in the Rockies

Michael J. Jenkins [1,*]**, Elizabeth G. Hebertson** [2] **and A. Steven Munson** [2]

[1] Department of Wildland Resources, Utah State University, Logan, UT 84322, USA

[2] US Department of Agriculture, Forest Service, Forest Health Protection, Ogden, UT 84403, USA;
E-Mails: lghebertson@fs.fed.us (E.G.H.); smunson@fs.fed.us (A.S.M.)

* Author to whom correspondence should be addressed; E-Mail: mike.jenkins@usu.edu;
Tel.: +1-435-797-2531; Fax: +1-435-797-3796.

Abstract: Spruce beetle outbreaks have been reported in the Rocky Mountains of western North America since the late 1800s. In their classic paper, *Spruce Beetle in the Rockies,* Schmid and Frye reviewed the literature that emerged from the extensive outbreaks in Colorado in the 1940s. A new wave of outbreaks has affected Rocky Mountain subalpine spruce-fir forests beginning in the mid-1980s and continuing to the present. These outbreaks have spurred another surge of basic and applied research in the biology, ecology and management of spruce and spruce beetle populations. This paper is a review of literature on spruce beetle focusing on work published since the late 1970s and is intended as an addendum to *Spruce Beetle in the Rockies*.

Keywords: *Dendroctonus rufipennis*; spruce beetle; Engelmann spruce; central Rocky Mountains

1. Introduction

The fundamental research on the biology, ecology and management of spruce beetle, *Dendroctonus rufipennis* Kirby (Coleoptera: Curculionidae, Scolytinae), in the central Rocky Mountains was conducted in Colorado following an extensive outbreak on the White River Plateau in the 1940s. Schmid and Frye [1] provided a comprehensive synthesis of this research in their classic

paper, *Spruce Beetle in the Rockies*, much of which is relevant and widely accepted by resource managers today.

Since the late 1980s, spruce beetle has affected over 180,000 ha of Engelmann spruce (*Picea engelmannii* Parry ex Engelm) in forests throughout the US Forest Service, Intermountain Region [2]. Recent spruce beetle outbreaks in Utah alone have resulted in the deaths of over 1 million spruce trees and the loss of over 90% of the large spruce component in affected stands [3,4] (Figure 1). Just over 500,000 ha of spruce forests have been affected in Colorado and Wyoming since 1996 [5].

Figure 1. Spruce beetle outbreak on the Wasatch Plateau (1985–1995), Manti-LaSal National Forest, Utah (Photo: A. Steven Munson).

These outbreaks have precipitated a surge in new basic and applied research aimed at clarifying our understanding and/or to fill knowledge gaps. Schmid and Frye [1] cited Wygant and Lejeune [6] who stated "all known major outbreaks originated from stand disturbances such as blowdown". Recent research, however, has shown that the mechanisms contributing to the occurrence of severe spruce beetle outbreaks are more complex. The unprecedented scale of the current outbreaks also suggests that warming temperatures attributed to climate change and the region-wide susceptibility of spruce in the spruce-fir zone have had a significant impact on outbreak occurrence [7–9].

This review synthesizes literature published since *Spruce beetle in the Rockies*, and can serve as an addendum to that classic publication. It was not the intent of this review to restate findings previously summarized by Schmid and Frye [1], but rather to expand and incorporate recent findings into the existing body of literature for foresters, forest health professionals, resource managers, and researchers to use into the future. However, we did cite earlier papers or gray literature if it provided context or information that would clarify new findings. We may have also interpreted results from our own perspectives and decades of cumulative experience in observing and managing spruce and spruce beetle in the Intermountain West. Our review is largely limited to findings from the central Rocky Mountains. However, it was at times necessary to discuss literature from other geographic regions of North America or for other bark beetle species. Werner *et al.* [10] reviewed the literature describing spruce beetle research and management conducted in south-central Alaska. Our goal was to be exhaustive in our literature search, but we may have failed to find all relevant references or chosen not to include some references where results may have been redundant. Research is ongoing and new publications will likely follow this review.

2. Historic Spruce Beetle Outbreaks

2.1. Methods to Determine the Occurrence of Spruce Beetle Outbreaks

The unprecedented scale of recent spruce beetle outbreaks in the central Rocky Mountains and Alaska prompted research to construct historic outbreak chronologies to better understand how, or if the spatial and temporal dynamics of spruce beetle populations might be related to climate change, past fire exclusion and suppression policies, and decreased forest management. Initial outbreak chronologies were derived from historic documents [7]. Beginning in the 1930s, extensive ground surveys and aerial survey methods enabled foresters and entomologists to document a relatively large number of spruce beetle outbreaks throughout the western US [7,11]. Relatively few reports of spruce beetle outbreaks, however, existed prior that time, preventing the construction of long histories needed to investigate potential relationships.

Spruce beetle outbreak chronologies have recently been extended with the development or refinement of environmental proxy measures. The occurrence of spruce beetle outbreaks and other disturbance events in Alaska and Colorado dating back to the 1700s has been determined from chronologies constructed by utilizing tree-ring release patterns, dates of spruce beetle-induced tree mortality, and years since stand establishment [4,7,12–18]. Hart *et al.* (2013) [19] utilized a combination of both historical documents and tree-ring records in a multiproxy approach to determine the history and synchrony of spruce beetle outbreaks in northwestern Colorado. The examination of lake sediment cores for spruce beetle macrofossils, and for decreases in spruce pollen coincident with increases in non-host pollen has been used in the attempt to construct chronologies of historic spruce beetle outbreaks dating back to the Holocene [20].

2.2. The Frequency and Extent of Historic Outbreaks

Appendix Table A1, modified from Hebertson and Jenkins [7], provides a chronology of historic spruce beetle outbreaks reported in Utah and Wyoming from circa 1900 to 2012. This chronology reports 28 outbreak years in the 112 year chronology, leaving a total of 84 non-outbreak years. Although the frequency of outbreak initiation dates varied, on average, outbreaks within a given geographic area were first reported once every 19 years. The exceptions were locations on the Wasatch Plateau in south-central Utah, the Aquarius Plateau in southern Utah, and the Markagunt Plateau in southwestern Utah where the average return interval of outbreak dates was 73 years. The frequency of outbreak dates on these plateaus was similar to the occurrence of historic outbreaks in northwestern Colorado where the median number of years between outbreaks at a site was 75 years [19]. Studies of spruce beetle outbreak synchrony across sites in northwestern Colorado, however, indicated that spruce beetle outbreaks were more likely than not to have occurred within 17 years of another outbreak [19], a finding consistent with outbreak return intervals from Utah and Wyoming [7]. Four periods of broad-scale spruce beetle outbreaks occurring from 1843 to 1860, 1882 to 1889, 1931 to 1957, and 2004 to 2010 were also evident in the northwestern Colorado chronology [19]. The latter two periods of broad-scale spruce beetle outbreaks are also evident in chronologies constructed for Utah and Wyoming (Appendix Table A1) and from historic documents for forests in New Mexico and Arizona [7].

Brunelle *et al.* (2008) [21] demonstrated that the presence of mountain pine beetle, *D. ponderosae* Hopkins, macrofossil remains in lake sediment cores could be used to date mountain pine beetle outbreaks in the northern Rocky Mountains back to the Holocene. Morris and Brunelle [22] and Morris *et al.* [23] analyzed pollen and other indicators in lake sediment cores to identify potential spruce beetle outbreaks in southern Utah. Applying these methods, Morris *et al.* [20] were able to successfully identify the severe spruce beetle outbreak that occurred on the Wasatch Plateau from mid-1980s through the early 1990s. However, the absence of a pollen release similar to that observed following this outbreak indicated that another outbreak of equal severity had not occurred on the Wasatch Plateau over the previous ~750 years [20].

3. Taxonomy

Wood [24] established the proper scientific name of spruce beetle, *Dendroctonus rufipennis* (Kirby), in 1969. The generic and specific epitaph have remained unchanged, however, the systematic positions of bark beetles and their closest relatives is still a matter of debate. Disagreement in taxonomic classification of bark beetles revolves around the relative importance of genetic and morphological characteristics, and their proximity to characteristics of weevils. Coleopterists formerly grouped bark beetles in the distinct family Scolytidae of the superfamily Curculionoidea [24,25] separate from the weevil family, Curculionidae. The family Scolytidae has since been reduced to the subfamily Scolytinae within the weevil family [26–29]. Although some taxonomists prefer the former classification [30,31], most experts in North America have adopted the new taxonomy based on most recent publication [32,33]. However, because of the unique ecological role of bark beetles in forest ecosystems, many experts disagree with the taxonomic change and stress the greater utility for management by separating bark beetles from weevils [34]. The development of new tools and molecular techniques may help clarify bark beetle systematics although taxonomy based solely on genetics may not always be appropriate [34].

4. Phylogeny

Research has increasingly employed genetic techniques such as mitochondrial DNA (mtDNA) gene sequencing, amplified fragment length polymorphisms (AFLP), nuclear gene sequencing, and microsatellite analysis in bark beetle phylogeographic studies to identify the origin of species or revise species boundaries, estimate divergence times of bark beetle lineages, and infer adaptions to local environments and patterns of range expansion [35–37].

Maroja *et al.* [37] utilized mtDNA and microsatellite data to examine the genetic structure of spruce beetle populations throughout their range and reconstruct spruce beetle phylogenies. The results of their study revealed the existence of three major spruce beetle groups that have been isolated since the early to mid-Pleistocene. Two northern groups, primarily associated with white spruce, extend west to east from Alaska to Newfoundland. Populations in these two groups likely originated from a single parent species and are probably interbreeding. Spruce beetle populations in the Intermountain region belong to the third group and primarily infest Engelmann spruce in the Rocky Mountains. However, spruce beetle populations in Utah and Arizona comprise a subgroup very distinct from populations found in Colorado, Montana, Washington, and British Columbia. This finding suggested that the

migration of spruce beetle populations in the Rocky Mountain group probably followed a northward post-glacial route along the eastern slope of the Rocky Mountains with no migration to the west [37].

Although little gene flow has occurred between the Rocky Mountain group and the two northern groups subsequent to their initial divergence, the results of this study provided evidence that secondary contact between overlapping Rocky Mountain and northern populations in the Pacific Northwest has resulted in some gene exchange and a consequent reconnection of these two groups [37]. Maroja *et al.* [37] suggested that the divergence and persistence of spruce beetle lineages may be attributed to reproductive isolation resulting from both physical barriers, such as repeated episodes of habitat fragmentation, and intrinsic barriers such as host specialization and/or pheromones (production, chemistry and activity) that limit gene exchange.

The existence of very divergent lineages in spruce beetle populations, in different geographical regions that inhabit specific species of spruce, raises the possibility that these populations also exhibit substantial genetic differentiation in life history or behavior [37]. Studies to further elucidate how genetic similarities or differences between spruce beetle populations relate to overlapping distributions of host trees may provide forest health professionals and land resource planners with useful management information such as the appropriate formulation, deployment, and timing of pheromones, in addition to the scale, type, and timing of silvicultural treatments [37].

5. Biology and Ecology

Spruce beetles (Figure 2a–c) interact with many other organisms and their abiotic environment. As with other bark beetle species, the dynamics of spruce beetle populations are influenced by interactions of both endogenous and exogenous factors [38]. Exogenous, or density-independent, factors include the occurrence of both random and non-random events such as blowdown and seasonal weather patterns. Endogenous, or density-dependent factors, act by positive and negative population feedbacks which may occur immediately (first-order feedback) or lag behind the generation time of spruce beetle (second-order feedback) [39]. Examples of endogenous factors include the availability and susceptibility of host trees, the suitability of habitat, inter- and intraspecific competition, beneficial and antagonistic associates, and natural enemies [38]. Exogenous and endogenous factors may directly or indirectly affect spruce beetle populations and are not mutually exclusive. Recent research has provided greater understanding of how these complex interactions influence populations.

Figure 2. Spruce beetle adult (**a**) (Photo: Megan O'Donnell and Andrew Cline, California Department of Food and Agriculture, Bugwood.org); spruce beetle eggs (**b**) (Photo: A. Steven Munson); spruce beetle larvae and pupae (**c**) (Photo: A. Steven Munson).

(**a**)   (**b**)   (**c**)
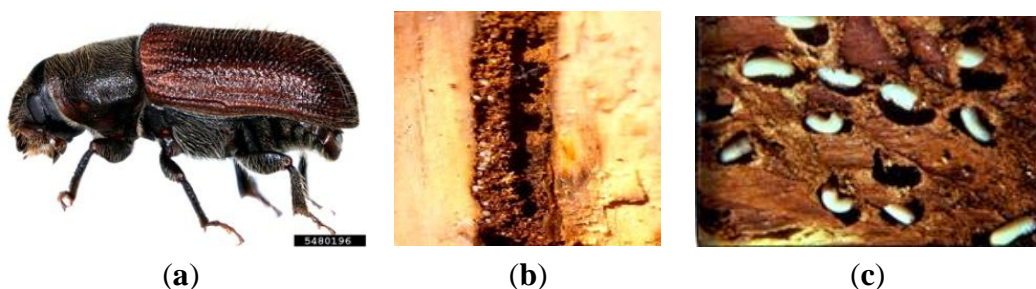
5.1. Exogenous Factors

5.1.1. Temperature

As poikilotherms, spruce beetle population growth and survival are highly sensitive to thermal conditions [9]. Earlier investigations indicated that seasonal temperatures could accelerate or shorten life cycles and consequently influence population growth [40]. Spruce beetle must diapause (overwinter once as adults) in order to reproduce, and may complete their life cycle in one, two, or possibly three years [1]. A semivoltine life cycle (one generation per two years) generally occurs at locations where relatively cool summer conditions retard larval development prior to the arrival of cold fall temperatures and beetles enter a prepupal diapause to overwinter [41]. Under warm conditions, spruce beetles may develop to pupal and adult stages by fall resulting in the univoltine (one generation per year) life cycle [41,42].

Hansen *et al.* [43] investigated the physiological basis for the flexibility in spruce beetle voltinism and found cool temperatures (≤15 °C) will not induce diapause during or before larval instar III. Life cycle regulation was also not dependent on developmental temperature thresholds imposed during specific life stages. However, instar IV larvae held at a cold temperature (≤15 °C) required a significantly longer time to pupate providing evidence of diapause induction during the prepupal stage [43]. Further study revealed that larvae allowed to mature more than ten days past the instar IV molt, pupated when placed at 15 °C [44]. Additionally, developmental delays indicative of diapause induction occurred in instar III through mid-instar IV larvae reared at this same temperature.

Linear models developed from cryophase threshold experiments indicated that a temperature of 13.6 °C should cause a 50% incidence of diapause induction within the population. Other experiments indicated that the induction of diapause occurs only with prolonged exposure (>40 days) to cold temperatures during instar III through instar IV. Early instar IV larvae exposed to cold temperatures for less time only experienced small to minor delays and resumed development with the return to favorable temperatures. This finding suggests that prepupal diapause is a continuous process rather than a discrete event [44].

By comparing short day and long day treatments in both diapause inducing and averting constant temperature regimes, Hansen *et al.* [44] also verified that photoperiod (day length) alone was insufficient for diapause induction in spruce beetles. They found this result sensible given that bark beetle life cycles are largely completed within the inner bark tissues of host trees in the absence of light.

This body of research revealed how specific air and subcortical temperature thresholds can influence life cycles within the same tree or other host material (*i.e.*, windfall *versus* stumps) within a stand [45,46]. Spruce beetle possesses the genetic potential for varying life histories, and temperatures above and below 15 °C, in addition to the timing and duration of thermal inputs during instar III through instar IV, determine whether life cycles follow univoltine or semivoltine developmental pathway [44]. Also, temperature induces diapause independently of photoperiod.

This information has also been used to model tree- or stand level proportions of univoltine beetles as a function of air temperature, and to parameterize a maximum likelihood estimation model of temperature-dependent instar IV developmental rates, including the effect of diapause [47,48].

Temperature-based voltinism models for example, indicated that the cumulative air-temperature hours above 17 °C elapsed from 40 to 90 days after peak flight best estimated the proportion of univoltine *versus* semivoltine broods [47]. These outputs were consistent with temperature regimes (August temperatures averaging 16.8 °C over a three-year period prior to outbreak) found important for the occurrence of historic outbreaks in Utah and Colorado [7]. Land managers can use these models to forecast spruce beetle population trends and associated spruce mortality.

Hansen and Bentz [45] compared the reproductive capacity of univoltine beetles with that of semivoltine beetles and re-emerged parents collected in both spring (June) and fall (November). They measured the weight and lipid content (indicative of beetle quality) of new adults in each group, and conducted a field experiment to test the flight capability of re-emerged parents. Potential brood production among the three groups was determined by measuring gallery characteristics, the number of eggs laid, egg length, larval development rates, and brood survival after 90 days. Hansen and Bentz [45] found that the weight and lipid content of beetles was highly variable among these three groups. However, the overall egg production and other measured brood characteristics including larval development rates and total brood survival did not differ among the three groups. Hansen and Bentz [45] also found that a least some re-emerged parents were capable of flight and that peak flight occurred approximately one week earlier than that of all other beetles.

The results of these studies provided evidence that new univoltine broods can contribute to accelerated rates of spruce beetle population growth, particularly when combined with broods of semivoltine and re-emerged adults [45]. Hansen and Bentz [45] suggested that a shorter life cycle also reduces the exposure of spruce beetle broods to adverse weather conditions and predation. Epidemic populations of spruce beetle, however, often persist long after temperatures return to near normal suggesting that genetically controlled, density-dependent behavioral mechanisms more likely determine spruce beetle replacement rates during outbreaks [49].

The survival of overwintering spruce beetles is closely related to winter temperatures with death occurring below critical winter thresholds. Early laboratory studies conducted in Colorado indicated that temperatures below ~26 °C were sufficient to kill spruce beetle adults while larvae died at ~34 °C [50]. Critical low temperature thresholds were slightly higher in interior Alaska [51]. To prevent the formation of ice in their body tissues or fluids, spruce beetles accumulate cryoprotectant compounds such as glycerol to lower supercooling points [51]. Spruce beetle larvae generally have higher tolerance to extreme cold than adult beetles, although both these life stages are more freeze-tolerant than pupae [50,51]. The vigor of host trees does not appear to affect the ability of spruce beetles to produce cryoproctectants or influence rates of winter mortality [52].

5.1.2. The Availability and Suitability of Host Trees

In general, spruce beetle behaves as a facultative parasite primarily colonizing host material with minimal or reduced defenses including newly fallen, stressed, and weakened trees [49,53]. Endemic populations of spruce beetle have often been associated with root disease mortality centers. Root diseases compromise host tree defenses in addition to root system integrity that contributes to the incidence of fallen trees [54]. Approximately 80% of dead conifers in root disease mortality centers in subalpine forests of Colorado were infested by bark beetles and borers [55]. Pockets of spruce

beetle were associated with Armillaria (*Armillaria ostoyae* (Romagnesi) Herink) root disease centers in south-central Utah [56]. Lewis and Lindgren [57] found that tomentosus root disease (*Inonotus tomentosus* (Fr.:Fr.) S. Teng) helped maintain endemic populations of spruce beetle in British Columbia, although the incidence of root disease and tree condition was not generally related to rates of spruce beetle attack during epidemics. Conversely, Lewis and Lindgren [57] observed that spruce beetle avoided attacking severely infected trees [57]. The inconsistency in these observations indicate that further research is needed to elucidate potential cause and effect relationships between spruce beetle and the suite of root disease fungi commonly encountered in the mortality centers.

Endemic populations of spruce beetle typically inhabit the well-shaded aspects of newly fallen host trees [49,58,59]. This material lacks defenses necessary for deterring colonization and provides favorable thermal and moisture conditions for brood survival [49,58]. Winter snow cover may also insulate spruce beetles from lethally cold temperatures and protect brood from predation by woodpeckers and squirrels [59,60].

Disturbances that produce an abundance of fresh downed host material including timber harvesting, blowdown, landslides and snow avalanches have been implicated in the occurrence of most historic outbreaks [7,49,58,59]. Large outbreaks on the Payette National Forest in Idaho that resulted in mortality of 350,000 trees over 90,000 ha were attributed to major windthrow events in 1981 and 1982 [7]. Dymerski *et al.* [3] reported that an outbreak on the Wasatch Plateau, Utah during the late 1980s–1990s resulted from a large landslide that toppled hundreds of Engelmann spruce within susceptible stands. In a study of this same outbreak, Hebertson and Jenkins [58] speculated that major snow avalanches produced brood material that was both temporally and spatially suited for spruce beetle colonization.

Large disturbance events, however, have not always resulted in outbreaks of spruce beetle [7]. Kulakowski and Veblen [61], for example, found evidence of an extensive blowdown event in Colorado dating to 1934 that did not result in increased spruce beetle-caused tree mortality. These observations suggest that host tree conditions, stand structure, weather, and population levels must all align with the fallen tree event for the initiation of outbreaks.

5.2. Endogenous Factors

5.2.1. Host Tree Condition and Selection

Healthy trees possess defenses lethal to bark beetles. The successful colonization of host trees for brood production consequently requires bark beetles to first overcome host tree defenses. Like other bark beetle species, spruce beetle relies on pheromone-mediated behaviors to increase attacks until attack densities are sufficient enough to kill the host tree [62,63]. The condition of host trees determines their suitability for attack.

Female spruce beetles locate suitable host trees possibly using both olfactory (volatile chemicals such as specific pheromones and allomones) and visual cues [64–66]. Females of incipient populations prefer to attack trees lacking adequate defenses and only initiate attacks on healthy trees after this resource has been depleted. During outbreaks, spruce beetles have demonstrated a preference for large diameter trees that presumably have higher nutritional quality than smaller trees [1,38,49,67]. This

preference is unlike that of mountain pine beetle that may initially avoid attacking large diameter hosts due to their more pronounced defenses [68]. Host selection may also occur at random during flight, where after encountering a tree, the beetle tests its suitability for colonization by short-range olfaction or gustation [69].

After landing, bark beetles may use chemical and tactile cues for orientation [70]. Spruce beetles tend to land more on the north aspect of spruce boles [71]. The thermal and moisture conditions of inner bark tissues beneath shaded bole aspects are favorable to the production of spruce beetle broods and may deter competition with other bark beetle species, particularly, *Ips pilifrons* Swaine (Coleoptera: Curculionidae, Ipinae) [58,59,71].

Upon selecting a suitable host tree, pioneering females produce aggregation pheromones that attract males and other females to the host tree. The production of anti-aggregation pheromones serves to limit attack densities reducing intra-specific competition [62,63]. Anti-aggregation pheromones may also 'switch' the focus of beetle attacks on more resistant trees, although the mode of operation differs among species [62,72]. Hard [62] found that strong aggregation pheromone plumes initially concentrate spruce beetle attacks in localized areas around focal trees, although spruce beetle anti-aggregation pheromones less effectively elicit switching behaviors compared to other bark beetle species such as mountain pine beetle.

The influence of host tree condition on spruce beetle selection behavior, however, may not be as important as once believed. Moeck *et al.* [73] observed that approximately equal numbers of western pine beetle (*D. brevicomis* LeConte) landed on healthy and diseased ponderosa pines (*P. ponderosa* Dougl. ex Laws.) and non-host species that were either eventually colonized or rejected. Spruce beetle has been similarly observed to attack and kill lodgepole pine (*Pinus contorta* Dougl. ex Loud.) associates in stands during eruptions, although the quantity and quality of broods produced from this species, or the extent to which they contribute to spruce beetle population dynamics has yet been quantified [1]. More recent studies have shown that during outbreaks most, if not all, of the susceptible host type is attacked regardless of vigor [3,67].

Spruce beetle population densities may also influence host selection behavior. In field and laboratory experiments, Wallin and Raffa [49] found that like female beetles of endemic (low density) populations, female beetles of epidemic (high density) populations preferred felled host material with low defenses. However, epidemic population females more readily initiated attacks on healthy and previously attacked trees compared to endemic population females.

In further laboratory tests, Wallin and Raffa [49] observed that individual female beetles reared from endemic populations were most attracted to media similar to that of host trees. Female beetles reared from epidemic populations selected media amended with alpha-pinene concentrations characteristic of healthy trees more readily than endemic population females. Most importantly, the attraction of beetles to media generally increased with the addition of other beetles and this behavior was most pronounced for in epidemic population beetles. Media amended with the highest concentration of alpha-pinene repelled beetles of both populations, while intermediate concentrations of monoterpenes elicited entry and gallery construction of both populations. Endemic population females constructed significantly longer galleries than epidemic population beetles across all concentrations of monoterpenes. These selection and gallery construction behaviors were inherited by offspring when reared in a common environment [49].

Wallin and Raffa [49] also found that spruce beetles with higher total lipid content were more attracted to media amended with alpha-pinene, regardless of their population phase. Beetles from incipient populations, however, had 34% less total lipid content than endemic beetles. Intra-specific competition resulting from high brood densities may explain this result. Shifts in selection and gallery construction behaviors resulting from lower total lipid content may ensure that beetles will fully exploit available host resources during outbreaks [49].

Based on these results, Wallin and Raffa [49] suggested that as the density of a population increases during an outbreak, spruce beetles attack healthy well-defended trees not because they must become less selective. Rather, increased intra-specific competition modifies their ability to discriminate between host resources thus allowing them to exploit a broader range of host resources. Expanding host feeding breadth contributes to population growth leading to the further exploitation of host trees. The different selective pressures that host defenses and competition exert on endemic and eruptive population phases may explain the density-dependent responses of spruce beetle, in addition to lipid stores that affect flight duration and the consequent potential for aggregation on the tree bole. These genetically-based, host acceptance behaviors interacting with environmentally induced cues, serve to maintain heterogeneity among endemic and eruptive population phases [49].

5.2.2. Spruce Beetle Associates

Spruce beetle interactions with fungi, bacteria, mites, and nematodes, as well as competitors and natural enemies through either density-dependent and/or density-independent mechanisms can also contribute to population fluctuations [53,74,75]. Many recent studies indicate that these interactions are complex and often involve multiple species that can serve to facilitate or perturb each other's interactions [76].

Fungi including blue-staining mycelial species and yeasts are among the most pervasive associates of bark beetles [77]. Like other bark beetle species, spruce beetle has long been known to vector several species of blue-staining fungi in the genera *Ophiostoma*, *Leptographium*, and *Ceratosystis* [53]. These fungi are introduced into living host trees during the attack process and subsequently develop in the phloem and sapwood [53]. Bark beetles carry fungal spores in specialized structures, or on the outer surfaces of their bodies. Spruce beetles lack mycangia (specialized mouthparts), but rather transport fungal spores in uncovered cuticular pits on the head, prosternum, or elytra [78].

Experts generally regard bark beetle relationships with blue-staining fungi as either symbiotic or mutualistic benefiting either associate, or both, respectively [53]. Bark beetle vectors aid in the success of fungal dissemination and introduction into new host trees. Feeding bark beetles likely gain nutritional benefits through fungal colonization. The combined colonization of host trees by both bark beetles and blue-staining fungi may accelerate the death of host trees through the drying of damaged vascular tissues and consequent disruption of water conduction, by compromising constitutive and induced defense mechanisms, and toxin release [53,79].

The prominence of blue-staining fungal associates and the degree to which these fungi affect spruce beetle-host systems often varies from strongly positive to strongly negative [74,80,81]. Six and Bentz [77] found that *Leptographium abietinum* (Peck) Wingfield was the most common species isolated from widely distributed spruce beetle populations, including populations from Utah and

Colorado. Aukema *et al.* [82] and Cardoza *et al.* [76] also found *L. abietinum* on the majority of spruce beetles collected from populations in Alaska. These findings were consistent with those of earlier studies [78,83].

Bentz and Six [80] found that *L. abietinum* and other blue-staining fungi isolated from the exoskeleton of spruce beetle contained relatively high concentrations of ergosterol (24β-methycholesta-5,7,trans 22-trien-3β-ol), a sterol not manufactured by insects, yet vital to their normal growth, metamorphosis, and reproduction. The content of ergosterol in host tree phloem naturally infested by spruce beetles was also significantly higher than in uninfested phloem. These findings suggested that spruce beetle life stages not only obtain important nutrients from phloem tissues, but also from their fungal associates [80].

This finding was supported by Cardoza *et al.* [74] who observed that the weight gain of male and female spruce beetles feeding on malt extract agar plugs infected by *L. abietinum* was higher than those feeding on uninfected plugs, although gains were not significantly different. Female spruce beetles feeding on phloem tissue infected with *L. albietinum* experienced lower mortality rates. However, the fungus negatively affected spruce beetle gallery construction and oviposition [74].

Cardoza *et al.* [74] also identified several mite species associated with spruce beetle in Alaska, the most common being *Histiogaster arborsignis* (Acari: Acaridae). This mite species preferentially fed and oviposited on *L. abietinum*. In some cases, it was also observed feeding on spruce beetle eggs. Earlier studies discussed in Schmid and Frye [1] suggested that some mite species were predaceous on spruce beetle although this finding was never verified. Consequently, although spruce beetle may derive some nutritional benefits from the fungus, the relationship may also have antagonistic effects [74].

In Alaska, Aukema *et al.* [82] found some evidence that the prevalence of *L. abietinum* varied with the population phase of the insect. The frequency of this fungus was higher on beetles collected from incipient and epidemic phase populations than beetles collected from sites where beetle population phases were in transition, although this relationship was not always significant. They also found the probability that individual beetles carried *L. abietinum* varied inversely with the co-occurrence of other fungal associates during the different population phases.

Ophiostoma piceae Davidson and Wells was commonly cultured from wood samples of host trees infested by populations of spruce beetles in British Columbia [84], as well as *Ceratocystis rufipenni* Wingfield, Harrington and Solheim, a member of the *Ceratocystis coerulescens* (Munch) Baski complex. Although the latter species has been considered a virulent pathogen in British Columbia and to a lesser extent Alberta [85], some refute this finding indicating that this species has not been directly isolated from spruce beetles [77,82]. The inconsistencies in these findings may be due to inherent difficulties with isolating this fungus [77]. Several minor or incidental *Ophiostoma* species have been found in association with spruce beetle, but their presence may be a result of cross contamination from other cohabiting scolytid species [77,82].

Other mycelial fungi that typically infect decaying wood may opportunistically colonize the galleries of spruce beetles and have antagonistic effects as the insect invades host trees [76]. Cardoza *et al.* [76] isolated two species of green-spored hyaline hyphomycetes in the genera *Trichoderma* and *Aspergillis* that decreased the survival and reproduction of spruce beetle. In this same study, they also identified several species of bacteria present in oral secretions of spruce beetle that

inhibited the growth of these fungi. Of these, the actinomycete, *Micrococcus luteus*, had the strongest inhibitory effect. Spruce beetles used their legs to spread oral secretions in the gallery space surrounding their bodies or as they entered fresh phloem. Cardoza *et al.* [76] suggested that this behavior might enhance the protective role of bacteria by confining the fungi, or preventing galleries from becoming infected during their construction.

Adams *et al.* [75] later exposed fungal associates of several bark beetle species to bacterial volatiles alone and bacterial volatiles in combination with the host volatile, alpha-pinene. Bacterial volatiles either stimulated or inhibited mycelial growth, or stimulated spore production of fungi. The strongest effects were induced by bacteria associated with bark beetles adapted to attacking living trees with vigorous defenses. Alpha-pinene served to amplify, reduce or reverse the interactions among bacteria and fungi [75].

Six and Bentz [77] most commonly found yeasts in association with spruce beetle. Safranyik *et al.* [84] found that yeast added to spruce beetle diets reduced time of spruce beetle development by half suggesting that yeasts may be required or have positive effects on the normal development of the brood.

Several species of nematodes were earlier reported to infest spruce beetle contributing to the decline of localized outbreaks [1]. Cardoza *et al.* [74] more recently described species of nematodes associated with spruce beetle in Alaska including new species they identified in several genera. These nematodes occurred in anhydrous clusters underneath the elytra, mainly attached at the proximal end, or within nematangia associated with the membranous wings [86]. Based on the results of their culturing assays, Cardoza *et al.* [74] found that the nematode associates of spruce beetle are largely microbial feeders for at least part of their life cycle with *Aphelenchoides* and *Bursaphelenchus* species observed feeding on *L. abietinum*, and *Parasitorhabditis* species thriving on unknown bacteria or yeast. It remained unclear to Cardoza *et al.* [74] whether the most common species isolated from spruce beetle was the species *Ektaphelenchus obtusus*, or a morph of a previously unknown species of *Bursaphelenchus*. The matter is considered important given that *Bursaphelenchus* is the genus containing the injurious pinewood nematode. Mite species in this same study were also observed to eat nematodes [74].

5.2.3. Natural Enemies

Although the recent studies of spruce beetle population dynamics has focused on the role of fungi and other spruce beetle symbionts, predators and parasitoids also impact spruce beetle populations. Schmid and Frye [1] summarized earlier studies of predaceous Coleoptera and Diptera species and Hymenoptera parasites known to kill high percentages of spruce beetles in the central Rocky Mountains. The most common predaceous species included the clerid beetles *Thanasimus undatulus* Say (Coleoptera: Cleridae) and *Enoclerus lecontei* Wolcott (Coleoptera: Cleridae), and the fly species *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae). The most common parasitoids were species in the Hymenoptera families Braconidae, Roptrocerus, and Cecidostiba. The importance of *M. aldrichii* was considered second only to woodpeckers (*Picoides* sp.) as a biological mortality agent of spruce beetles.

Although insect predators and parasites may help maintain spruce beetle populations at endemic levels, spruce beetle populations have erupted in spite of the presence of these agents, and these agents

have never been associated with the collapse of spruce beetle epidemics [1]. Studies investigating the role of arthropod associates of spruce beetle in south-central Alaska supported initial observations that interspecific competition with other scolytid bark beetles was more important than either insect predators or parasites in influencing spruce beetle population density [87].

Based on a review of the literature, Fayt *et al.* [88] suggested that woodpeckers (*Picoides* sp.) play a significant role in the regulation of spruce beetle populations. The literature indicated that woodpeckers caused between 19% and 98% beetle mortality depending on spruce beetle population densities and larval size. These values considered the direct effects of woodpeckers on spruce beetle mortality and the indirect effects including accelerated desiccation of host trees, competition with other predators and parasites, higher caloric requirements associated with cold temperatures, or lethally high temperatures [88].

Fayt *et al.* [88] also found that increases in woodpecker densities were generally related to stand structure following disturbances where spruce beetle populations were likely to build. In particular, the three-toed woodpecker (*P. tridactylus*) tended to aggregate in areas recently disturbed by fire and blowdown. Typically, predatory woodpeckers were reported to reach a peak density in the first two years following fire before declining rapidly, although winter densities increased up to eight years in some post-fire stands. Fire effects and other factors were reported to affect the availability of both bark beetles and other insect prey. During pan-epidemics, however, woodpecker densities decreased due to increased territorial interactions. Based on these behaviors, Fayt *et al.* [88] suggested that woodpeckers reaching infested stands at the initiation of outbreaks would result in greater percentages of spruce beetle mortality. The literature reviewed indicated that the population response of woodpeckers to spruce beetle densities also increased during the breeding season, but peaked from August to December when juvenile birds dispersed from their natal habitats. Other studies cited indicated that in spite of population densities, woodpeckers generally tended to ignore young beetle larvae due to their small size. These reports suggested that the proportion of spruce beetle mortality caused by woodpeckers was generally related to spruce beetle availability and their size attained at times of dispersal [88]. Reported rates of woodpecker-caused larval mortality were greater in semi-open stands compared to dense stands. Fayt *et al.* [88] suggested that this finding may be related to influences of voltinism on spruce beetle.

The red squirrel (*Tamiasciurus hudsonicus*) is another vertebrate species known to consume spruce beetle. Pretzslaw *et al.* [89] observed that red squirrels eat spruce beetle larvae if the availability of conifer seed is low, the density of spruce beetle-infested trees is high, or to satisfy some nutritional requirements. They also observed that red squirrels typically searched for spruce beetle larvae in infested trees located near middens, and ate approximately four spruce beetle larvae per minute. Populations of red squirrels may help keep endemic populations in check, particularly if unfavorable conditions such the loss of seed sources during outbreaks increases the squirrels' reliance on spruce beetle as a food resource [89].

5.3. Landscape and Climate Influences on Spatiotemporal Population Dynamics

Climate variability and the structure and composition of stands across forested landscapes are both known to influence the potential for spruce beetle population growth, and the spread and duration of

outbreaks [4,8,9,44,90]. Weather-related mechanisms for example, directly affect spruce beetle population dynamics through the influence of temperature on cold tolerance (winter survival) and life history strategies that lead to the synchrony of population emergence [9,38,91], or indirectly by predisposing host trees to attack [92]. Forest heterogeneity influences the development of spruce beetle outbreaks by limiting population spread to susceptible stands [8,93]. The synchronous occurrence of outbreaks at multiple spatial and temporal scales evident in spruce beetle outbreak histories from the central Rocky Mountains alludes to the influences of both weather and forest conditions [7,15,16,19]. Only recently, however, has research explored potential linkages between climate and forest conditions and their influence on the spatiotemporal patterns of spruce beetle populations.

Recent research suggests that regional or hemispheric-scale atmosphere circulations that determine climate (temperature and drought) act as the main extrinsic drivers of spruce beetle outbreaks. Over interannual time scales (approximately one to three years) El Niño Southern Oscillations (ENSO) combined with late-summer drought, contributed to spruce beetle outbreaks in Alaska [18]. Over multidecadal scales (approximately 40 years), the cool-phase Pacific Decadal Oscillation (PDO) preceded outbreaks regardless of ENSO phase.

Hart *et al.* [19] examined the climatic conditions that influence broad-scale spruce beetle outbreaks in northwestern Colorado by comparing periods of outbreak and non-outbreak years with annual and multidecadal ENSO, PDO and Atlantic Mutltidecadal Oscillation (AMO), in addition to short-term (monthly and seasonal) climatic variability factors including temperature, precipitation, the Palmer Drought Severity Index, and vapor pressure deficit. They found that annual periods of the positive AMO phase and high summer vapor pressure deficits were the most important predictors of broad-scale outbreaks. This suggested that spruce beetle outbreaks could be attributed to temperature as well as a reduction in tree defenses due to drought-induced tree stress [19].

DeRose and Long [67] characterized the spatial and temporal patterns of spruce beetle-caused tree mortality in Engelmann spruce-fir stands on the Markagunt Plateau in southern Utah. They suggested that site characteristics and the spatial variability of host susceptibility, combined with forcing from exogenous factors such as temperature anomalies, influenced spruce beetle population success and host tree mortality. The results of their spatial and temporal autocorrelation tests revealed that spruce beetle populations did not originate and spread from one location (epicenter). Rather, eruptions occurred synchronously in multiple locations alluding to an over-riding influence of temperature. These findings were consistent with studies examining the contribution of stand conditions and temperature to the occurrence of spruce beetle outbreaks in Alaska [17,90]. Early increases in mountain pine beetle populations similarly occurred in multiple epicenters across western Colorado at the onset of a widespread outbreak in the late 1990s [94]. DeRose and Long [67] suggested that the connectivity of uninfested and infested stands might have influenced spatiotemporal spread patterns.

In a second study, DeRose *et al.* [95] further explored the relative contribution of temperature and stand conditions to fluctuations in spruce beetle populations. They used spruce beetle habitat data collected by USDA Forest Service, Forest Inventory and Analysis (FIA) coupled with climate data to predict (presence/absence) current and future distributions of spruce beetle in spruce of the Interior West, USA. Both spruce beetle habitat and climate variables were associated in predictions of spruce beetle presence or absence. While minimum cold season temperature and maximum warm season temperature were important predictors, the percentage of Engelmann spruce and mean basal area of

stands were the most influential in the model. Although temperatures may directly control beetle population dynamics, DeRose and Long [95] asserted that regardless of temperature conditions, the occurrence of spruce beetle outbreaks relied on the availability of suitable habitat as determined by stand structure and composition. This assertion was consistent with Chapman *et al.* [94] who found that the expansion of mountain pine beetle outbreaks in western Colorado relied more on the homogeneity of stands and absence of cold temperature than drought.

6. Spruce Beetle and Fire

A very long return interval, high-severity fire regime typically characterizes Intermountain spruce-fir forests [96–99]. Elevations exceed 2500 m in the spruce-fir zone and climates are generally cool and moist [100]. These conditions primarily influence the flammability of small diameter fuels (1 and 10 h fuels) reducing the ignition risk (chance of fire starting) and initial spread of fire. Fire weather conditions conducive to extreme fire behavior are also limited to a few weeks in late summer during most years. As a consequence, the frequency of wildfires in spruce-fir forests is low with return intervals often >100 years [1,14,15,101–103]. The fuels complex that develops in spruce-fir forests between major wildfires naturally predisposes stands to high-intensity fire. The severity of these fires is based on their physical characters (rate of spread, flame length, intensity) and the fire adaptations of the vegetation. Engelmann spruce, subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., and other subalpine vegetation evolved with limited adaptations to fire and few trees survive [97].

6.1. Spruce Beetle Effects on Forest Fuels

Alterations in fuel complexes as a result of widespread spruce beetle-induced tree mortality may increase potential fire intensity, severity, and occurrence [1,50,101,104–106]. However, only relatively recently has research systematically focused on an understanding of bark beetle, fuel and fire interactions [105–107]. Studies have been conducted in bark beetle-affected stands of Engelmann spruce [4,12,13,108,109], lodgepole pine [110–112], whitebark pine [113,114], and Douglas-fir [115–117]. In general, bark beetle outbreaks result in a reduction in the number of live trees, average stand diameter, canopy base height, and the quantity and quality of canopy foliage. During early stages of the outbreak there is an increase in the amount of dead canopy foliage and in turn a transfer of needles and some fine twig material from the conifer canopy to the forest floor such that surface litter amounts increase at the expense of canopy fuels [105,109]. Total surface fuel accumulation amounts to nearly a one-to-one transfer of aerial needles to surface litter, minus whatever decomposition occurs over the period of needle shed [118]. Overstory tree mortality not only results in a pulse of needle litter and small diameter woody fuels to the forest floor during the epidemic phase, but also a release of shrubs and forbs in the early part of the post-epidemic [109]. The accumulation of coarse woody fuels is dependent upon the rate at which dead overstory snags fall to the surface. There is considerable variation in coarse woody fuel accumulation depending on stand structure, species composition, site, soils, physiography, and incidence of root disease and when compared to other bark beetle/host ecosystems [119,120].

6.2. Implications for Fire Behavior

It has been difficult to correlate spruce beetle-caused tree mortality and fuel bed alterations with increases in the number of ignitions, fire risk, or changes in fire behavior [12,13]. Mesic and moist understories largely comprised of forbs and shrubs have been shown to increase after epidemics [109] and may inhibit fire behavior [13]. Bigler *et al.* [121] concluded that pre-fire stand structure has a greater influence on fire risk and severity than the impact of spruce beetle outbreaks alone. Likewise, real time fire weather, drought, and the point of ignition have been shown to have greater influence on fire extent than the pre-fire conditions resulting from a spruce beetle outbreak [122]. However, once trees are attacked there may be periods of increased foliage flammability due to changes in foliar moisture and volatile terpene content causing increased likelihood of crown fire initiation [106,108,111]. Additionally, important physical changes in stand structure during and following spruce beetle epidemics may alter potential fire behavior. For example, overstory removal typical of widespread spruce beetle mortality can change microclimatic conditions through a combination of factors, including increased solar insolation, decreased relative humidity, and wind sheltering [123]. Higher wind speeds on the surface fuels can potentially increase surface fire spread rate [124,125] and increased solar radiation can raise fuel temperatures leading to increased fireline intensity [124–127].

6.3. Surface Fire Behavior

Surface fire flame lengths and rates of spread, based on Rothermel's [128] reformulated surface fire model generally predict greater flame lengths and rates of spread over the course of the bark beetle rotation [106]. The predicted surface fire behavior is similar to what others have reported in forests affected by mountain pine beetle [129] with increases in fire intensity in the post-epidemic condition class due to increases in fuel loading and decreases in fuel moisture. Differences in surface fire behavior are due to slight increases in fuel load in the 1, 10, and 100 h fuel categories coupled with decreased fuel moisture based on unshaded fuel moisture values.

Significant increases in shrub cover and loading documented by Jorgensen and Jenkins [109] could pose a significant barrier to surface fire spread and result in over prediction in the post-epidemic fuel bed. Fire prediction software packages that rely on Rothermel's [128] surface fire spread model do not adequately capture the potential heat sink effect that live shrubs and forbs (live moistures > 200%) may have on surface fire behavior. Sandberg *et al.* [130] acknowledged the issues associated with the moisture damping coefficient in Rothermel's [128] model and suggested substitution of other moisture damping options in the future as new research sheds light on the contribution of moist live fuels to surface fire behavior.

6.4. Crown Fire Behavior

Crown fires are the most intense type of wildland fires and result from the interaction between surface and canopy fuels. Crown fires in bark beetle-affected landscapes present significant challenges to fire managers [108] and produce important long-term ecosystem impacts [101].

The distribution, quantity and quality of canopy fuels largely influence overall crown fire behavior. Inventoried stand level attributes measured by Jorgensen and Jenkins [108] showed significantly lower

amounts of live available canopy fuel and consequently lower live canopy bulk densities in epidemic and post-epidemic classes. This condition will likely decrease the probability of active crown fire initiation and spread. This result has been reported widely by others in bark beetle-affected stands [111,112,128–130] and reflects the significant decrease in available live canopy fuel load in stands with high levels of overstory mortality. Canopies in the epidemic class have proportionately more dead foliage than canopies in the endemic or post-epidemic classes. Crown-to-crown fire potential in such stands is influenced by the moisture content and chemistry of dead foliage [107]. Dead fuel is often more flammable than live foliage due to a lower heat of ignition and processes that control moisture absorption and retention [107,131]. Higher wind speeds are required to carry crown fire through the epidemic stands because dead foliage falls relatively quickly from bark beetle-attacked spruce [107,132]. Seasonal drying and prolonged drought may also cause both live and dead fuels to become even more flammable [133]. No current fire prediction system based on Van Wagner's [134] crown fire initiation model adequately captures the influence of these dead fuels, which may be important during a relatively short period before the needles drop (*i.e.*, less than 2 years).

It is unlikely that active crown fire would develop in epidemic and post-epidemic classes except under extreme weather conditions that drive large fire growth in these forests [135]. Overall crown fire behavior remains uncertain where there are mixtures of live and dead fuel considering differences in moisture and volatile composition [108,131,136]. Thus, caution is urged in interpreting crown-to-crown potential results in epidemic stands given the uncertainties surrounding crown fire spread in forests with significant dead foliage. Additionally, there are inherent biases within the crown fire behavior models [137]. Cruz and Alexander [138] and Alexander and Cruz [139] reviewed studies that predicted crown fire potential and concluded that there is a significant under prediction bias based on the traditional crown fire initiation and spread models [134].

As stands altered by spruce beetle activity mature, they may again become more susceptible to active crown fire spread as spruce and fir regeneration results in lower canopy base heights and increases the potential for surface fire to transition into a passive crown fire [134]. Simard *et al.* [112] suggested that the contribution of decreased foliar moisture content from dead aerial fuels was not significant in active crown fire spread in epidemic mountain pine beetle-affected lodgepole pine forests. However, Simard *et al.*'s [112] use of foliar moisture content may not be appropriate in stands with significant dead foliage. Van Wagner's [134] crown fire spread model used in their analysis is not designed to simulate fire spread in canopies with significant dead overstory fuels.

Although spruce beetle-induced tree mortality alters fuel complexes, these alterations alone may not necessarily increase the susceptibility of spruce-fir forests to wildfire [102]. The cool, moist weather conditions in the Intermountain subalpine zone often limit fire occurrence and behavior except under extreme weather conditions such as drought [12,101,120,121,135]. Bebi *et al.* [12] also found that the frequency of lightning-caused fires did not increase following spruce beetle outbreaks [12]. Buechling and Baker [99] concluded that periods of summer drought were most influential in the occurrence of large fires in high elevation forests in north central Colorado. When weather parameters are moderate or low, fuels can be more influential in determining fire behavior [135]. Thus, the flammability of spruce/fir forests is not only a product of available fuels but is also a function of drying, wind, plant species composition, ignition points and the fuel complex of adjacent patches of the landscape [140].

Crown fire behavior is only one concern facing fire managers in bark beetle-affected conifer forests. Managers must also consider how bark beetle tree mortality influences fire suppression operations such as line construction rates and spotting and firefighter safety especially involving snags and safety zones. A holistic approach involving fire behavior prediction, fire suppression operations, and firefighter safety must be considered in determining how bark beetle outbreaks will affect resistance to fire control in conifer forests [141].

7. Management

7.1. Impacts of Spruce Beetle-Induced Tree Mortality

As with other tree-killing bark beetle species, spruce beetle-induced tree mortality has been associated with both ecological and/or economic benefits and costs. Endemic-phase populations of bark beetles have an important role in decomposition and nutrient recycling over long temporal scales by removing older, weaker individuals from stands of trees [142,143]. Insects, fungi, and other microorganisms often colonize the inner bark of dead trees to exploit more easily digested and nutritious tissues as food [144,145]. Woodpecker species and red squirrels consume spruce beetles for food [59,60,88,89]. Dead trees benefit snag dependent wildlife species by providing nesting habitats [142].

Large-scale, intense bark beetle outbreaks can adversely affect watershed, timber, critical wildlife habitat, aesthetics, and recreational resources [142,146]. The loss of trees in recreation settings reduces shade, screening, and aesthetics thus compromising visitor experiences. Dead trees also pose potential hazards to public safety requiring routine tree hazard inspections and maintenance [147]. In addition, costs associated with dead tree removal along road corridors and maintained trails can also be excessive.

In areas managed for values other than recreation, the mortality of overstory spruce results in a modification of stand structure and species composition. For example, a spruce beetle outbreak on the Markagunt Plateau, Utah killed 93% of overstory Engelmann spruce during the 1990s [4]. Where stands were largely dominated by Engelmann spruce prior to the outbreak, species composition shifted to subalpine fir, aspen (*Populus tremuloides* Michx.), and limber pine (*Pinus flexilus* James). Subalpine fir comprised the majority (62%) of understory (trees <5.0 cm) followed by aspen (32%) and Engelmann spruce (6%). The broad age range of understory trees suggested that understory recruitment had been relatively continual prior to the outbreak [4]. Given the magnitude of overstory Engelmann spruce loss and the paucity of Engelmann spruce regeneration, 300–400 years may elapse before Engelmann spruce-dominated forests were restored. These findings support previous research conducted by others [14,15,102,108,148–150].

Few widely scattered large diameter spruce escape infestation during epidemics affecting management objectives to maintain structural and compositional diversity. The elimination of seed sources not only influences species availability, but may also result in a corresponding reduction in genetic diversity [148]. The loss of viable, natural seed sources and the lack of bare mineral soil following beetle disturbance may deter the establishment of seedlings requiring artificial regeneration of the site [4].

Schmid and Frye [1] questioned the approach that "control efforts usually began after an infestation had caused substantial tree mortality…", where recommendations for spruce beetle management involved salvage logging and strategies for reducing the high beetle populations in standing infested trees and logging residue. Rather, Schmid and Frye [1] suggested that the management of spruce beetle populations should be done in the decades preceding outbreaks by integrating beetle management into forest plans to reduce stand susceptibility and create stands with some level of resistance to spruce beetles. Options available to resource managers today are not substantially different than those available in the 1970s. Along with various resource objectives, the social and political climate has changed resulting in how spruce beetle populations may be managed.

7.2. Detection and Evaluation

Spruce beetle epidemics are most common in overmature stands where average diameter at breast height (dbh) exceeds 60 cm, but can be sustained in large pole (20–30cm dbh) and immature stands [6]. Windthrow events that occur in susceptible stands may result in outbreak populations of this insect. Scattered windthrow in late winter or spring is most conducive to population increases [58,151]. Windthrown trees should be sampled in late July–August following adult flight to determine attack densities in the downed material using a sampling scheme developed by Schmid [59]. Logging residue may also contribute to spruce beetle population increases. Safranyik and Linton [71] developed a line intersect sampling method to determine the density and bark area of logging residue susceptible to spruce beetle.

Spruce beetle populations are often detected through aerial surveys conducted by federal and state personnel [152]. Unfortunately, the visible signature of fading foliage is associated with trees successfully attacked the previous year and current mortality is not visible from the air. In addition, the window to observe the yellow-green fading needles is small; often 4–6 weeks before the majority of the needles have dropped to the forest floor. Because aerial detection surveys are ocular estimates of mortality, the aerial observers often underestimate the mortality percentage within mapped polygons. The utility of using satellite imagery to map bark beetle-caused mortality associated with the mountain pine beetle is well-documented in the literature [153]. It is also difficult to distinguish mortality caused by this insect *versus* other causes of mortality, and it has not been shown to be an efficient or cost effective technique to spatially record areas of spruce beetle infestation [154].

The development of the digital sketchmapping system, an adaptation of GeoLink software, GPS, mobile pen computers, and flat panel display provides a robust aerial mapping system. This system enables the aerial observer to collect data using a digital topographic image as background coverage, draw the pest infestation polygons directly onto the flat panel display, and quickly enter the required annotations for the GIS database [155]. In spite of errors of omission, aerial surveys conducted from a fixed wing aircraft using either a grid or contour pattern has continued to be the most cost effective method to record spruce beetle caused mortality over large landscapes.

Ground surveys provide a more comprehensive method for capturing current spruce infestations especially on smaller landscapes. Unlike recording older spruce mortality from an aerial platform, ground surveys capture currently infested trees that will not fade until the following summer. These often consist of systematic ground surveys comprised of line transects with fixed or variable radius

plots. The systematic survey strives to estimate the total number of beetle-killed trees with a sampling error of less than 25 percent, determine the infestation trend in the infested trees, and the susceptibility of the green trees remaining in the stand. A comprehensive ground survey may also consist of line transects recording infested or dead spruce trees within 10 m on each side of the transect and installing fixed or variable radius plots at 100 or 200 m intervals to capture stand attributes. Data on currently infested trees will indicate the number of trees killed and their distribution by diameter class. Since the transect lines are systematically arranged over the infested area, survey results will also provide some indication of the distribution of the infested trees within the surveyed landscape.

Although aerial and ground surveys provide a measure of tree mortality caused by this insect, several experimental designs have been conducted to measure spruce beetle population densities. Studies completed by Knight [156] determined the mean number of attacking beetles required to kill a standing tree with a specific breast height diameter. Hansen *et al.* [157] developed a method using baited funnel traps to estimate tree mortality and associated population phase of spruce beetle. Model predictions associated with trap results suggest that funnel trap captures can be reliably used to estimate relative levels of tree mortality, expressed as population phase.

Hazard rating systems such as those in FINDIT [158], an easy to use program to assess insect and disease effects from stand collected data, are often used by forest health specialists to evaluate stand conditions conducive to the growth and spread of damaging agents. "Hazard" or "susceptibility" measures are independent of the beetle population level and include site or stand characteristics that affect its likelihood of attack and damage by bark beetles. "Risk" includes a measure of the beetle population within and in the vicinity of the stand in conjunction with its susceptibility [159]. Risk is a function of tree/stand susceptibility and "pressure" imposed by bark beetle populations. Pressure is the magnitude of the bark beetle population affecting a stand as determined by the number of currently infested trees and their proximity to the stand being assessed. Pressure relates to the likelihood of bark beetles entering a given stand. A "high-hazard" stand can exist with little risk when bark beetle populations remain low. Conversely, a "low-hazard" stand can have moderate risk when populations of damaging agents are high [97,160]. Outbreak populations of bark beetles will likely infest stands rated high or moderately susceptible as outbreaks intensify. Beetles may infest stands rated low susceptibility when populations have reached high levels, or when they have depleted all suitable host type elsewhere.

A hazard or susceptibility rating system for spruce beetle developed by Schmid and Frye [161] is based on the average dbh of live spruce >25 cm, the basal area (BA) of the live stand, the percentage of live spruce in the stand and the physiographic location of the stand. Stands considered most susceptible to spruce beetle attack include those located in drainage bottoms with basal areas exceeding 34 m^2/ha, a live spruce component >60%, and average spruce diameters >40 cm dbh. Steele *et al.* [162] expanded the Schmid and Frye [161] hazard rating system and included site index of the dominant species as a variable for hazard rating spruce stands in central Idaho forests. However, even in mixed species stands, outbreak populations of the beetle can spread into dispersed pockets of host type and affect isolated susceptible individual trees. Hansen *et al.* [163] indicate that although the Schmid and Frye [161] model remains valuable for identifying susceptible stands, it might be improved by considering (1) spruce stand density index (SDI)—the control of growing stock, through initial spacing or subsequent thinning, to achieve specific management objectives [164], or spruce BA

rather than *total* BA; and (2) the density of spruce stems >28 cm dbh rather than the average diameter of spruce larger than 25 cm dbh. Schmitt and Powell [165] developed rating methodology for spruce beetle specifically designed to be compatible with photo-interpreted information and other remote sensing data sources. Data from stand reconnaissance surveys (walk-through exams) could also be used if appropriate tree measurements are collected.

7.3. Indirect Control

7.3.1. Prevention Strategies

Where active bark beetle populations exist, susceptible stands are at risk for infestation. Prevention strategies offer the greatest likelihood of reducing the long-term susceptibility of stands by creating a mosaic of structures, age classes, and species mixtures [67]. Traditionally, thinning (density management) has been the preferred strategy for bark beetle management in western forests [8,143]. Thinning is the selective removal of trees to benefit the quality of the stand [166]. Thinning effectively reduces a particular host resource base that supports bark beetle populations, reduces competition for water and nutrients, and disrupts the effectiveness of pheromone communication [167]. The higher temperatures in thinned stands also reduce beetle survival and alter attack behavior of the insect [1,168–170].

Empirical data addressing the efficacy of thinning treatments to mitigate spruce beetle effects is limited. Holsten *et al.* [146] indicated thinning stands maintained tree vigor and provided some resiliency to spruce beetle attack in Alaska. To reduce the long-term susceptibility of uninfested stands to spruce beetle, Alexander [171], based on studies compiled by Schmid and Frye [1], recommended density management strategies. These included partial cutting to remove the larger, overmature spruce leaving average spruce diameters around 30 cm dbh, decreasing mean stand basal areas to 18 m^2/ha, and reducing the spruce component to ≤65%. Thinning strategies would also promote natural regeneration and the growth of trees in smaller diameter classes to create the structural, species and age-class diversity necessary for perpetuating spruce and achieving other desired management objectives [171].

A retrospective assessment of partial cutting to evaluate the effects of spruce beetle-caused mortality by Hansen *et al.* [163] found that treated stands had fewer infested stems and less infested basal area than untreated stands as well as smaller proportions of infested stems and basal area. Most of this difference was associated with the smaller diameter classes (8–28 cm) with little difference in larger stem survivorship.

Uneven-aged prescriptions for spruce stands will not prevent losses caused by the spruce beetle, but will mitigate the effects of an outbreak in a treated area. An uneven-aged prescription may provide an average dbh of 19 cm, an SDI of 35 percent of maximum, and a basal area of 30 m^2/ha. Shaw [172] describes the method most commonly used to derive an SDI, and shows that the variables used to derive SDI in the case of uneven-aged stands must be carefully selected. The summation method should be used to calculate SDI if the management objectives are uneven-aged or irregular stand structures.

Table 1 provides an example of post-harvest diameter class distribution where a full range of diameter classes is the objective for an uneven-aged prescription. This prescription will generally meet several resources objectives (e.g., visuals, wildlife, *etc.*) while reducing stand density to a lower degree of full site utilization. Small, 0.1 ha openings will promote spruce regeneration within these uneven-aged systems. These small, spatially created canopy gaps may favor regeneration of shade tolerant Engelmann spruce [173]. Stand entry should occur before the stand reaches 60 percent maximum SDI to sustain the lower spruce beetle hazard rating. Where logging activities occur Schmid [174] developed guidelines for handling logging residuals that included cutting the tree as close to the ground as possible to reduce stump height (preferably <0.5 m) and limbing cull logs and tops and repositioning tops and cull logs away from shade and left unpiled unless they are to be burned.

Table 1. Example: Uneven-aged stand attributes for low hazard stand.

Mid-point DBH (cm)	Stand Density Index	Basal Area (m^2/ha)	Trees per Hectare
5	15	0.9	473
15.2	50	5.6	127
25.4	60	7.4	144
35.5	60	8.3	84
45.7	50	3.3	48
Total	235	25.5	876

Undesirable consequences of thinning treatments include visual and site impacts, and probable damage to residual trees increasing the potential for infections by root disease and decay fungi. Avoiding management activities in those portions of stands where root disease is prevalent may minimize infections. If necessary, root diseased areas can be treated favoring the most disease tolerant species. Depending on the thinning treatment, stands would also lose some percentage of large diameter overstory trees. Both beneficial and adverse impacts to wildlife species might occur. The production of green slash would necessitate implementing post-harvest treatments to mitigate potential colonization of host material by secondary beetles such as spruce engraver beetles particularly if treatments coincide with beetle flight periods. Post-harvest treatments should also address reducing hazardous woody fuels. Spruce-fir stands have an increased potential for blowdown in wind prone locations. This would necessitate monitoring treated areas on an annual basis to remove any susceptible and infested host material until the residual stand is windfirm.

7.3.2. Silvicultural Suppression Strategies

When bark beetle populations threaten valuable resources, other silvicultural alternatives can be used to address susceptible and/or infested stands. Although the suppression strategies described independently below can be employed to address spruce beetle populations, Bentz and Munson [175] used a combination of suppression treatments to suppress a building population of spruce beetle in northern Utah that included sanitation/salvage, trap trees, and baited funnel traps. Unless all susceptible hosts are removed to address bark beetle populations, repeated entries are often required to

suppress bark beetle populations. Repeated stand entries increase costs, may damage residual vegetation, and increase the potential for windthrow [100].

7.3.2.1. Sanitation

Sanitation treatments involve the removal of currently infested and susceptible host trees [146]. The removal of large diameter trees reduces stand densities and alters residual stand structure. To minimize the probability of re-infestation, particularly where risk remains high, sanitation treatments should address the entire susceptible host component [176]. Created openings may promote some age class diversity in treated sites. Stands to consider for sanitation treatment would include either uninfested or infested stands where (1) the stand still has a susceptible host component at risk to bark beetle attacks; (2) the majority of the infested landscape can be treated; and (3) bark beetle populations are not at outbreak levels on adjacent landscapes [175].

7.3.2.2. Salvage

Salvage treatments involve the removal of currently infested and dead trees from the stand or landscape. The primary treatment objective is to suppress localized bark beetle populations with a secondary objective of recovering some economic value before severe checking occurs within the tree bole [166].

Salvage treatments are most effective in stands or on landscapes where infestations remain small and the treatment will remove most, if not all of the infested trees within the affected landscape. However, salvage treatments are often combined with sanitation to suppress beetle populations [97]. Treatment success decreases significantly with rapidly expanding bark beetle populations. Openings created in stands could predispose residual trees to blow down, particularly within the spruce-fir type. This treatment would not reduce the susceptibility of stands to subsequent bark beetle attacks and may require monitoring and additional entries to treat or remove downed host material, or newly infested standing trees [176].

7.3.2.3. Sanitation/Salvage

A combination of sanitation and salvage treatments is often used to remove currently infested, dead, and susceptible trees (Figure 3). Sanitation/salvage treatments are designed to reduce bark beetle populations in stands with low, but building populations and decrease stand susceptibility. In some stands, particularly spruce-fir, host trees may occur in dense clumps (basal area exceeding $23m^2$). In addition to removing infested trees, selectively cutting susceptible trees to reduce average diameter and mean basal areas to a desired level will reduce residual clump susceptibility. Tree selection in patches could also favor non-host species. Benefits of this treatment would include deriving some commercial value from harvested timber and creating greater species and structural diversity. If spruce beetle populations are successfully suppressed, this treatment provides long term sustainability and maintains a mature tree class structure within the treated sites. Undesirable consequences of this treatment would include loss of large diameter trees, probable damage to residual trees, and increased windthrow potential.

Figure 3. Residual spruce-fir stand following a spruce beetle sanitation/salvage sale, Unita-Wasatch-Cache National Forest, Utah (Photo: Doug Page, Zone Forester, Bureau of Land Management).

In stands where susceptible host trees comprise more than the recommended percentage of basal area for desired management objectives, the following silvicultural options are possible:

1. Remove all infested and susceptible trees from the entire stand area leaving the average diameters and mean basal areas of the host tree component within desired ranges (*i.e.*, spruce diameter < 25cm, mean basal areas ≤ 28 m^2/ha) [162,171]. This would accomplish bark beetle management objectives while deriving commercial value from the timber harvested. Species and structural diversity would also result with residual trees available to replace those removed from the overstory. Both beneficial and adverse impacts to wildlife species might occur. Undesirable consequences of this treatment would include more extensive site impacts and visual impacts, damage to existing regeneration, loss of structural diversity, an increased potential for windthrow and the creation of heavy fuel loads.

2. Remove less than the recommended basal area of infested and susceptible host trees species throughout the management area. This alternative would not afford complete suppression with significant loss of large diameter spruce highly probable in the long term. Fuel loads would also increase over time, in addition to dead trees providing a source of inoculum of root disease fungi on the site [177]. Some commercial value would be derived, however, and certain wildlife species would benefit from the presence of infested trees, snags, downed woody material and the created diversity.

7.4. Direct Suppression Strategies

High value stands or trees growing in unique environments or under unique circumstances may be considered for short-term treatments designed to protect trees from spruce beetle attack. These could include trees in residential, recreational, or administrative sites.

7.4.1. Chemical Insecticides

Preventative applications involve chemical insecticides sprayed directly on the bole of susceptible hosts before spruce beetle flight (May). Insecticide treatments are often initiated to protect high value

trees if building or epidemic populations of spruce beetles exist in the area. Multiple applications may be required during the course of an outbreak. Insecticide treatments are applied with ground-based sprayers at high pressure (e.g., ≥2241 kPa) to the tree bole. Insecticide applications are applied to all bole surfaces up to a height of ~11 to 15 m until runoff to ensure thorough coverage of the root collar and exposed roots. The amount of insecticide formulation (water and insecticide) applied varies with tree architecture, tree size, equipment, and applicator, among other factors, but ranges between ~15 to 30 L per tree [178–180]. Bole sprays are typically applied in the fall to avoid access issues in the spring and spring runoff affecting "no spray" buffers to protect non-target aquatic organisms. In addition, most if not all of the adult flight has been completed by the fall.

Carbaryl (e.g., Sevin® SL and Sevin® XLR Plus), an acetylcholinesterae inhibitor, is commonly used to protect trees from spruce beetle attack. It is the most extensively studied active ingredient registered for use [181], and still the most effective, economically viable, and ecologically compatible insecticide to protect individual trees from bark beetle attack [180,182].

Pyrethroids, synthesized from petroleum-based chemicals and related to the potent insecticidal properties of flowering plants in the genus *Chrysanthemum*, are also registered for use to protect individual trees from spruce beetle attack. Permethrin (e.g., Astro® and Dragnet®, among others) and bifenthrin (e.g., Onyx®) are also used as preventative treatments for spruce beetle. However, unlike carbaryl which provides two seasons of protection, most research indicates only one field season of protection can be expected with pyrethroids [180,183].

Applied correctly, failures in efficacy are rare. However, when failures occur, they are often associated with inadequate coverage, improper mixing, improper storage, and/or improper timing (*i.e.*, applying treatments to trees already successfully attacked by spruce beetle) [178]. Removing obstructing limbs on the lower portion of the tree bole will improve treatment efficacy. Larger diameter trees (≥50 cm dbh) are difficult to treat effectively due to spray height limitations associated with most ground application equipment. With outbreak populations of the insect, spruce beetle attacks large diameter trees above the spray height killing that portion of the tree not treated (Figure 4).

Figure 4. Engelmann spruce topkill due to inadequate height coverage on the tree bole using ground application equipment to apply insecticide (Photo: A. Steven Munson).

Insecticide treatments applied to the tree bole are expensive over large areas and not a recommended strategy for general use. To minimize exposure of chemical residues, 10 mil plastic can be used to cover picnic tables, fire pit grates, and any other nearby facilities before application. Washing treated surfaces with a detergent solution will also mitigate chemical exposure to recreation site users.

Research is ongoing in an attempt to find a safer, more portable and longer lasting alternatives to bole applied insecticides by injecting small quantities of systemic insecticides directly into the lower bole. Shea *et al.* [184] evaluated the effects of acephate, dimethoate, and carbofuran delivered by Medicap implants in both unattacked and attacked spruce in Alaska. Tree mortality ranged from 60%–93% percent for all insecticide treatments with 100% mortality of the control trees. The insecticide treatments were determined to be inadequate in preventing tree mortality. An experimental formulation of 4.0% emamectin benzoate injected in late August in unattacked Engelmann spruce was ineffective for protecting individual trees from spruce beetle caused mortality in Utah [185] (Figure 5). However, the commercial formulation of TREE-age^TM is currently being evaluated by USDA Forest Service research entomologists and others by applying an early summer *versus* late summer treatment to unattacked Engelmann spruce in Utah.

Figure 5. Arborjet Inc. injection treatment used to apply insecticide directly into the tree bole [185] (Photo: A. Steven Munson).

7.4.2. Pheromones

Pheromones are message-bearing chemicals emitted by adult bark beetles and the host tree. Semiochemical-based research for bark beetle control has been widely studied [186–189] since the identification of the first bark beetle pheromones [190]. These chemical signals regulate the behavior of beetles during their mating and aggregating phases. Borden [191] discussed five principal means by which semiochemicals can influence population dynamics of bark beetles. These include, (1) mediation of aggregation and mass attack on new hosts; (2) cessation of aggregation and shifting of attack to uninhabited hosts; (3) induction of aggregation by competing species; (4) inhibition of aggregation by competing species; and (5) mediation of host finding by commensal and entomophagous insects.

Aggregation pheromones are chemical cues used by the insect to manipulate mating behavior. As a result, the pheromone attraction causes bark beetle aggregation that overcomes a host trees' defenses. Anti-aggregation pheromones serve to disrupt attraction after beetles have invaded host trees [192]. Pheromone treatments have been proposed where environmental and safety concerns prohibit chemical use (e.g., spray zone buffer near water corridors).

Methylcyclohexenone (3-methylcyclohex-2-en-1-one, or MCH) is an anti-aggregation pheromone produced by the spruce beetle [193]. MCH has been applied to reduce the numbers of spruce beetles attracted to infested logs and synthetic semiochemical lures [193–197]. However, MCH has not been effective in preventing the infestation of live trees [198] with one exception in Alaska, when it was dispersed using a microinfusion pump in areas with low spruce beetle population densities [199]. Ross *et al.* [200] conducted a paired plot study using MCH in southern Utah in sites with high spruce beetle population densities. Although they used an application rate twice the current recommended dose for Douglas-fir beetle [201], MCH was not effective in preventing host tree infestation. A subsequent study by Wallin and Raffa [49] demonstrated that spruce beetle host selection behavior changes with population density which may explain the different responses observed in field studies. MCH and green leaf volatiles have been tested for interrupting host location by spruce beetle [202,203]. Poland and Borden [204] in a multiple funnel trapping bioassay reduced spruce beetle catches in traps baited with frontalin and alpha-pinene up to 42% in the presence of synthetic (+)-exo-brevicomin and (+)-endo-brevicomin, aggregation pheromones of the sympatric species *Dryocoetes affaber* Mannerheim, (Curculionidae: Scolytinae). They also found that trap catches were reduced 85% by (±) or (+)-ipsdienol but not by (−)-ipsdienol. *Ips tridens* Wood, (Curculionidae: Scolytinae) a second sympatric species, produces both enantiomers of ipsdienol in its pheromone blend.

Spruce beetle is effectively attracted using either a two component lure (frontalin {1,5-dimethy-6,8-dioxabiocyclo[3.2.1]octane} + alpha-pinene) or a three component lure (frontalin + alpha-pinene + MCOL). The addition of MCOL (1-methyl-2-cyclohexen-1ol) substantially increased spruce beetle attraction in field studies [205]. Attractant formulations have been used to monitor spruce beetle activity, determine mortality and population phase of the insect described previously, and as a suppression tactic using baited Lindgren funnel traps [206] in conjunction with other sanitation treatments [175]. Attractants have also been used with the standing trap tree strategy described below.

7.4.3. Trap Trees

Trap tree strategies are often combined with other suppression tactics to reduce small and isolated populations of the insect. During endemic population phases, spruce beetle maintains populations in windthrown or diseased trees. Since the beetle prefers downed host material to standing green trees, trap trees are used as a suppression tactic. Spruce selected as trap trees are green, larger diameter trees (>40 cm dbh) felled to attract attacking adult spruce beetles. Until treated, trap trees should remain unbucked to prevent desiccation. Avoid falling trap trees adjacent to uninfested stands or adjacent to standing susceptible spruce spillover attacks and further tree mortality. Trap trees should be felled in the shade and left unlimbed [207,208]. They are most effective if felled in the spring before adult beetle flight [58]. Trap trees effectively attract beetles up to 0.4 km and less effectively up to 0.8 km [207].

Felled trap trees typically have greater mean attack densities than standing spruce [1] and often attract 10 times or more the number of adult beetles that attack standing trees, thus the number of trap trees requiredwill be less than the number of infested standing trees [208]. The number of trap trees felled also depends on the level of infestation and size of the infested trees. In static infestations, the number can range from 1–10 depending on the diameter of standing infested trees and the diameter of trap trees. Larger diameter trap trees absorb more beetles. In building infestations, the number of trap trees ranges from 1–5 based on the same parameters used for determining number of trap trees for static infestations [207,208]. In stands with heavy pockets of infestation, one trap tree per two to three infested standing trees is recommended. In centers of spruce beetle activity, clustering trap trees has proven effective, where two to four trees are felled 20 m apart to concentrate attacks.

Non-host trees baited with the attractant pheromone are also potential trap trees because reproduction is prevented and many parent adults die due to the pitch produced by the non-host tree [209]. Lethal trap trees, which are felled or standing host trees baited with the spruce beetle attractant and treated with an arboricide/insecticide, have had mixed results. Field tests conducted in Alaska and British Columbia on baited felled trees treated with monosodium methanearsentate (MSMA) had significant effects on attack density in British Columbia, but not in Alaska. The difference between the two locations may have been caused by lower temperatures and beetle population densities in Alaska [210].

Susceptible host trees adjacent to felled trap trees will often be attacked. Felling trap trees in sites comprised of non-host trees or small diameter host trees (<20.3 cm dbh) will reduce the number of spillover attacks on adjacent susceptible hosts. Trap trees not treated by the following spring before adult flight, will add to further tree mortality. To suppress beetle populations, all standing and down infested trees should be treated (burned, debarked or removed) before beetle emergence the following spring (Figure 6).

Figure 6. Log Wizard[TM] [211] used to peel bark from spruce beetle infested Engelmann spruce (Photo: A. Steven Munson).

7.4.4. Trap Trees (Standing and Baited)

Standing trap trees baited with an attractant pheromone (tree bait) are effective at absorbing beetles, but attract fewer beetles than downed trap trees [209] (Figure 7). Baiting standing susceptible green trees with aggregation pheromones is an effective method for attracting flying beetles and inducing attack. The baits are stapled on the north side of standing, green trees prior to flight. Secondary attraction to the treated tree often develops and it is not uncommon to experience adjacent susceptible trees also attacked. Tree baits are often deployed to focus beetle attacks into sites where trees can easily be treated and/or to reduce spread from infested sites. Where possible, trees should be baited close to active spruce beetle pockets (within 30–60 m), or within the pocket. Cluster baiting appears to maximize attraction. This method consists of baiting three trees spaced 15–30 m apart in a deltoid pattern within infested pockets. Once colonized, the baited trees are removed, or treated in the same manner as trap trees during the year of attack. Baiting strategies are most effective if used in units with isolated infestations in conjunction with sanitation treatments.

Figure 7. Standing baited Engelmann spruce trap trees marked in orange paint (Photo: A. Steven Munson).

7.4.5. Funnel Traps and Natural Baiting

This technique uses Lindgren funnel traps (12–16 tiered) [206] baited with a two component lure, frontalin and alpha-pinene, or three component lure, frontalin, alpha-pinene and MCOL. For the spruce beetle, three-component lures will attract more adult beetles [205], however, the effects of spillover are greater. If three-component lures are used, the minimum distance from a susceptible spruce to a baited trap should be 23 m. For the two-component lure, 15 m is recommended. In centers of infestation, funnel traps are deployed in clusters of three with individual funnel traps spaced 15 m apart. Funnel trap clusters are spaced at approximately 91 m intervals. To minimize spillover, funnel traps should be placed within clumps of non-hosts or dead trees. This is the least effective means of reducing beetle numbers, however, when used in conjunction with other suppression strategies, funnel traps will assist in reducing populations [175].

Hansen *et al.* [157] compared naturally baited trapping systems to synthetically baited funnel and fallen trap trees for suppressing pre-outbreak spruce beetle populations. Lures for the traps were fresh Engelmann spruce bolts or bark sections augmented by adding female spruce beetles to create secondary attraction. Previously, Hansen *et al.* [157] compared a naturally baited system ("bolt trap") with fallen trap trees and with synthetically baited funnel traps. Trap performance was evaluated by comparing total beetle captures and spillover of attacks into nearby host trees. Overall, the trap systems did not significantly differ in spruce beetle captures, however, bolt traps caught 6 to 7 times more beetles than funnel traps. Funnel traps with synthetic lures had significantly more spillover than either trap trees or bolt traps. They repeated the study with modifications that included an enhanced blend synthetic lure [157]. Trap captures were generally similar among naturally and synthetically baited traps, but naturally baited traps had significantly less spillover. Although labor-intensive, the bolt trap could be used to suppress pre-outbreak beetle populations, especially when spillover is undesirable.

7.5. *Vegetation Management Plans*

Comprehensive vegetation management plans should be the long-term goal of reducing the impacts of spruce beetle on spruce forests. Such plans will incorporate both long and short-term insect and disease strategies to provide land managers with ecologically appropriate and economically feasible treatments based upon resource goals and management priorities. Vegetation plans will also provide guidance for minimizing the adverse impacts associated with spruce beetle outbreaks while meeting resource objectives. Opportunities should be sought to identify stands where planting a mixture of native tree species would create an environment that supports greater diversity and reduces long-term insect and disease impacts.

Implementation of treatment strategies will require addressing the potential for hazardous fuel accumulations near or on private lands, high-value recreation sites, and transportation and utility corridors. Hazard tree inspections and dead tree removal can be designed and implemented in conjunction with wildland–urban interface fuel reduction programs.

Satisfying critical land-use objectives in the future will necessitate preparing cooperative strategies to restore and maintain the ecological integrity of forests affected today. Public awareness and education will be critical for successfully implementing selected spruce beetle treatment alternatives. As new information about spruce beetle conditions or management activities becomes available, education and outreach opportunities will increase. Cooperative efforts will be needed to develop educational outreach activities and materials that can be used to increase public awareness. These efforts will assist in increasing public support and understanding of the potential impact of spruce beetle outbreaks and associated management activities [212]. The success of any long-term spruce beetle management program will require an increase and/or redirection of funding toward future landscape level silvicultural treatments, restoration efforts, hazard tree removal, and reduction of hazardous fuels.

8. Summary

Spruce beetle is native disturbance agent of North American spruce-fir forests and primarily infests Engelmann spruce in the central Rocky Mountains. During outbreaks spruce beetle will also infest

lodgepole pine and blue spruce. Spruce beetle-caused tree mortality has been associated with both ecological and/or economic benefits and costs. Spruce beetle has an important role in decomposition and nutrient recycling, and providing habitat and food for wildlife. Large-scale, severe bark beetle outbreaks can adversely affect watershed, timber, critical wildlife habitat, aesthetics, and recreational resources.

Spruce beetle prefers to infest host material with reduced defenses and is commonly found inhabiting fallen host material produced by natural disturbances such as wind, snow avalanches, and landslides. Spruce beetle may also infest susceptible logging residues. Disturbances that produce an abundance of fallen host material may contribute to local outbreaks. Not all disturbance events, however, result in outbreaks. In these cases, insufficient numbers of spruce beetles may be available to exploit host material before it deteriorates. Endemic phase populations are also often associated with root disease mortality centers. Root diseases result in the failure of root systems and increase the likelihood tree fall. Pathogen-induced stress may predispose standing trees to spruce beetle attack. The nature of spruce beetle and root disease associations, however, remains poorly understood. Large-scale outbreaks have also been shown to erupt from multiple epicenters suggesting that weather influences, particularly temperature, has a more important influence in their initiation than disturbances. Spruce beetle only initiates attacks on healthy trees once non-defended host resources have been depleted.

Under certain conditions, endemic spruce beetle populations erupt. Sites across the central Rocky Mountains experience outbreaks approximately once every 75 years. However, outbreaks occur somewhere within a given geographic area once every 15 to 20 years. The occurrence and synchrony of historic broad-scale spruce beetle outbreaks in the central Rocky Mountains have been attributed to positive phases of AMO and drought. Climate, through direct temperature influences, determines spruce beetle life histories. Temperatures above and below 15 °C, and the timing and duration of thermal inputs during instar III through instar IV determine whether life cycles follow a univoltine or semivoltine pathway. Higher proportions of univoltine broods can accelerate rates of population growth. Warm winters increase the survival of overwintering broods. Drought-induced stress compromises host tree defenses thus indirectly affecting the suitability of host trees for spruce beetle colonization and brood survival.

Suitable habitat must exist for spruce beetle outbreaks to occur regardless of climate. Dense stands comprised of a high percentage of large diameter spruce are most conducive to outbreak initiation and population expansion.

Density-dependent population factors, particularly, intraspecific competition, the nature of defensive constituents in host trees, and the lipid stores of dispersing adults more likely influence spruce beetle population replacement rates during epidemics than temperature. Spruce beetle interacting with fungi, bacteria, mites, and nematodes, as well as, natural enemies can also influence fluctuations in populations. The influences of spruce beetle associates can either be beneficial or antagonistic. The most common blue-staining fungal associate of spruce beetle is *Leptographium abietinum*. Natural enemies may help regulate localized populations of spruce beetle, however, their presence or absence does not influence outbreak occurrence. Woodpeckers and the fly, *Medetera aldrichii*, are the most important biological mortality agents of spruce beetle.

Spruce beetle outbreaks affect ground, surface and aerial fuels in both live and dead fuel categories significantly altering the nature of the fuel bed. The effect of spruce beetle outbreaks can be immediate in terms of litter and fine fuels and last for decades as coarse woody fuel accumulates, and as

succession proceeds in post epidemic stands. Common wildland fire behavior models were not developed to predict fire behavior characteristics in bark beetle-affected fuelscapes and outputs, especially crown fire predictions, should be viewed with caution No definitive association between spruce beetle activity and crown fire behavior has been established. To the contrary post hoc analyses of spruce beetle outbreaks and fire occurrence has shown no clear relationship. Experimental fires and focused, expert observation of fire behavior in spruce beetle-affected stands could yield important information to establish relationships. Bark beetle outbreaks in western North American conifer forests have important effects on fire management beyond fire behavior. Resistance to fire control will increase in bark beetle-affects forests and operationally consideration must be given to fireline construction rates, spotting, snag mitigation and firefighter safety.

Spruce beetle management strategies include prevention, suppression and restoration activities. Prevention strategies often utilize silvicultural practices to modify stand conditions favorable to spruce beetle and should occur before populations reach unmanageable levels. By enhancing stand diversity and resiliency, prevention strategies can help avoid unacceptable resource losses, maintain or enhance resource objectives, and maximize revenue in the long term. Suppression strategies are usually implemented with building insect populations. When implemented during the initial stages of an outbreak, suppression activities can reduce population levels and the rate of insect spread. Treatment alternatives associated with suppression, however, are usually limited and applied at small scales. Treatments may not sufficiently modify stand conditions and the benefits are often short term. Restoration activities attempt to reestablish vegetation and promote the long-term resiliency of forests to insects and diseases.

The development of vegetation management plans incorporating both long and short-term insect and disease treatment strategies would provide guidance for minimizing adverse impacts and meeting resource objectives. A single treatment strategy generally does not address all resource values within a susceptible and/or infested landscape. Therefore, the selection of ecologically appropriate and economically feasible treatments should consider resource management priorities.

The literature cited has increased our understanding of spruce beetle biology, ecology and management. Important questions remain that provide opportunities for future research direction.

- How successful is brood production in lodgepole pine and blue spruce hosts? Does brood production from these hosts significantly contribute to population growth? How does blue spruce chemistry affect spruce beetle pheromones?
- How does the distribution and density of endemic phase spruce beetle populations affect the reliability of predicting if, where, or when populations might erupt on a given landscape?
- What is the role of natural enemies and spruce beetle associates, particularly fungi, in maintaining endemic populations of spruce beetle?
- What population levels exist in root disease mortality centers? Do root diseases affect the nutritional quality of trees for brood production?
- What are the specific mechanisms that incite endemic populations of spruce beetle to initiate attacks on healthy trees?
- What other density-dependent mechanisms influence spruce beetle population fluctuations?

- How can wildland fire behavior prediction systems be modified to accurately predict surface and crown fire behavior in bark beetle-affected conifer forests?
- What remote sensing technologies can provide reliable methods for detecting, monitoring and quantifying spruce beetle population trends?
- What are effective alternatives to direct suppression of spruce beetle populations?

9. Conclusions

Spruce Beetle in the Rockies is a comprehensive treatise on the biology, ecology and management of spruce beetle reflecting the knowledge and understanding as it existed in the late 1970s. The extent of the outbreaks in the US since 2000 indicates, however, that the recommendations of Schmid and Frye in the 1970s were not sufficiently applied at the landscape scale to mitigate the outbreaks of the last two plus decades. In the intervening decades management has focused on direct control and salvage logging as the mainstays of managing spruce and spruce beetle populations on public lands in the US. Effective management has been hindered by lack of timber harvesting infrastructure, cost *versus* benefit realities, required environmental analyses, appeals and court litigation, and lack of national public support for timber management programs [212].

The outbreaks have, however, provided current researchers with suitable field sites to conduct the research we have cited in this paper. This reflects in many ways the history of research on forest insect species that cause outbreaks resulting in economic losses. Research opportunities and funding follow outbreak cycles and once outbreaks subside these opportunities diminish, interest wanes, and the motivation and incentives for landscape-scale management decrease. It is our hope with this paper that we have provided the next generation of managers with research findings that can supplement *Spruce Beetle in the Rockies* and guide management activities/opportunities into the future. As it was in 1977, so it is today. We view the post-epidemic period as an opportunity to manage spruce stands in advance of the next outbreak to create stands with some level of resistance to spruce beetle.

Changing social mores and political agendas coupled with uncertain impacts of human population growth and demand on resources, invasive species and climate change will, however, challenge effective management like never before [212].

Conflicts of Interest

The authors declare no conflict of interest.

References

1. Schmid, J.M.; Frye, R.H. *Spruce Beetles in the Rockies*; General Technical Report GTR RM-49; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1977; p. 38.
2. Man, G. *Major Forest Insect and Disease Conditions in the United States: 2009 Update*; FS-952, USDA Forest Service, Forest Health Technology Enterprise Team: Washington, DC, USA, 2010; p. 28.
3. Dymerski, A.D.; Anhold, J.A.; Munson, A.S. Spruce beetle (*Dendroctonus rufipennis*) outbreak in Engelmann spruce (*Picea engelmannii*) in central Utah, 1986–1998. *West. N. Am. Nat.* **2001**, *61*, 19–24.
4. DeRose, R.; Long, J.N. Disturbance, structure, and composition: Spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah. *For. Ecol. Manag.* **2007**, *244*, 16–23.
5. Harris, J. Forest Insect and Disease Conditions Rocky Mountain Region (R2); R2 Conditions Report; US Department of Agriculture, Forest Service, Forest Health Protection, 2012; p. 10. Available online: http://www.fs.usda.gov/goto/r2/fhp/ (accessed on 31 October 2013).
6. Wygant, N.D.; Lejeune, R.R. Engelmann Spruce Beetle *Dendroctonus obesus* (Mann.) (=D. engelmannii Hopk.). In *Important Forest Insects and Diseases of Mutual Concern to Canada, the United States and Mexico, Canadian*; Department of Forest and Rural Development: Ottawa, Canada, 1967; Publication No. 1180, p. 248.
7. Hebertson, E.G.; Jenkins, M.J. Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. *Environ. Entomol.* **2008**, *37*, 281–292.
8. Fettig, C.J.; Klepzig, K.D.; Billings, R.F.; Munson, A.S.; Nebeker, T.E.; Negrón, J.F.; Nowak, J.T. The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. *For. Ecol. Manag.* **2007**, *238*, 24–53.
9. Bentz, B.J.; Régnière, J.; Fettig, C.J.; Hansen, E.M.; Hayes, J.L.; Hicke, J.A.; Kelsey, R.G.; Negrón, J.F.; Seybold, S.J. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience* **2010**, *60*, 602–613.
10. Werner, R.A.; Holsten, E.H.; Matsuoka, S.M.; Burnside, R.E. Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research. *For. Ecol. Manag.* **2006**, *227*, 195–206.
11. Furniss, M.M. *The History of Forest Entomology in the Intermountain and Rocky Mountain Areas, 1901–1982*; General Technical Report, RMRS-GTR-195; USDA Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2007.
12. Bebi, P.; Kulakowski, D.; Veblen, T.T. Interactions between fire and spruce beetles in a subalpine Rocky Mountain landscape. *Ecology* **2003**, *84*, 362–371.

13. Kulakowski, D.; Veblen, T.T.; Bebi, P. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *J. Biogeogr.* **2003**, *30*, 1445–1456.

14. Veblen, T.T.; Hadley, K.S.; Nel, E.M.; Kitzberger, T.; Reid, M.; Villalba, R. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *J. Ecol.* **1994**, *82*, 125–135.

15. Veblen, T.T.; Hadley, K.S.; Reid, M.S. Disturbance and stand development of a Colorado subalpine forest. *J. Biogr.* **1991**, *18*, 707–716.

16. Eisenhart, K.S.; Veblen, T.T. Dendrochronological detection of spruce bark beetle outbreaks in northwestern Colorado. *Can. J. For. Res.* **2000**, *30*, 1788–1798.

17. Berg, E.E.; Henry, J.D.; Fastie, C.L.; DeVolder, 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.

18. Sherriff, R.L.; Berg, E.E.; Miller, A.E. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. *Ecology* **2011**, *92*, 1459–1470.

19. Hart, S.J.; Veblen, T.T.; Eisenhart, K.S.; Jarvis, D.; Kulakowski, D. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* **2013**, doi:10.1890/13-0230.1. Available online: http://doi.org/10.1890/13–0230.1 (accessed on 17 November 2013).

20. Morris, J.; Brunelle, A.R.; Munson, A.S. Pollen evidence of historical forest disturbance on the Wasatch Plateau, Utah. *West. N. Am. Nat.* **2010**, *70*, 175–188.

21. Brunelle, A.; Rehfeldt, J.; Bentz, B.J. Holocene records of mountain pine beetle infestations in the US Northern Rocky Mountains. *For. Ecol. Manag.* **2008**, *255*, 836–846.

22. Morris, J.L.; Brunelle, A. Pollen accumulation in lake sediments during historic spruce beetle disturbances in subalpine forests of southern Utah, USA. *Holcene* **2012**, doi:10.1177/0959683612437870. Available online: http://hol.sagepub.com/content/early/2012/03/15/0959683612437870 (accessed on 20 November 2013).

23. Morris, J.L.; Le Roux, P.C.; Macharia, A.N.; Brunelle, A.; Hebertson, E.G.; Zachary, J.L. Organic elemental, and geochemical contributions to lake sediment deposits during severe spruce beetle *(Dendroctonus rufipennis)* disturbances. *For. Ecol. Manag.* **2013**, *289*, 78–89.

24. Wood, S.L. New synonymy and records of Platypodidae and Scolytidae (Coleoptera). *Gt. Basin Nat.* **1969**, *29*, 113–128.

25. Furniss, M.M.; Carolin, V.M. *Western Forest Insects*; Miscellaneous Publication No. 1339; USDA Forest Service, Pacific Northwest Forest and Range Experiment Station: Portland, OR, USA, 1980.

26. Marvaldi, A.E.; Sequeira, A.S.; O'Brien, C.W.; Farrell, B.D. Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea): Do niche shifts accompany diversification? *Syst. Biol.* **2002**, *51*, 761–785.

27. Marvaldi, A.E.; Morrone, J.J. Phylogenetic systematics of weevils (Coleoptera: Curculionoidea): A reappraisal based on larval and adult morphology. *Insect Syst. Evol.* **2000**, *31*, 43–58.

28. Kuschel, G.A. Phylogenetic classification of Curculionoidea to families and subfamilies. *Mem. Entomol. Soc. Wash.* **1995**, *14*, 5–33.

29. Lawrence, J.F.; Newton, A.F., Jr. Families and Subfamilies of Coleoptera. In *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*; Pakaluk, J., Slipinski, S.A., Eds.; Museum I Instytut Zoologii PAN: Warszawa, Poland, 1995; pp. 779–1006.

30. Morimoto, K.; Kojima, H. Morphological characteristics of the weevil head and phylogenetic implications (Coleoptera, Curculionoidea). *ESAKIA* **2003**, *43*, 133–169.

31. Wood, S.L. A reclassification of the genera of Scolytidae (Coleoptera). *Gt. Basin Nat. Mem.* **1986**, *10*, 1–126.

32. Triplehorn, C.A.; Johnson, N.F. *Borror and Delong's Introduction to the Study of Insects*, 7th ed.; Thomson Brooks/Cole: Belmont, CA, USA, 2005; p. 864.

33. *American Beetles, Polyphaga: Scarabaeoidea through Curculionoidea*; Arnett, R.H., Jr., Thomas, M.C., Skelley, P.E., Franks, J.H., Eds.; CRC Press: Boca Raton, FL, USA, 2002; Volume 2, p. 861.

34. Jordal, B.H. Reconstructing the Phylogeny of Scolytinae and Close Allies: Major Obstacles and Prospects for a Solution. In Proceedings of the Genetics of Bark Beetles and Associated Microorganisms: Third Workshop, Asheville, NC, USA, 20–21 May 2006; Bentz, B., Cognato, A., Raffa, K., Eds.; USDA Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2007; p. 45.

35. Bentz, B.J.; Pfrender, M.; Bracewell, R.; Mock, K. Genetic Architecture of the Differences in Fitness Traits among Geographically Separated *Dendroctonus ponderosae* Populations. In Proceedings of the Genetics of Bark Beetles and Associated Microorganisms: Third Workshop, Asheville, NC, USA, 20–21 May 2006; Bentz, B., Cognato, A., Raffa, K., Eds.; USDA Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2006; RMRS-P-45, p. 25.

36. Cognato, A.I. A Standard DNA Taxonomy for Insects. In Proceedings of the Genetics of Bark Beetles and Associated Microorganisms: Third Workshop, Asheville, NC, USA, 20–21 May 2006; Bentz, B., Cognato, A., Raffa, K., Eds.; USDA Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2006; RMRS-P-45, p. 11.

37. Maroja, L.S.; Bogdanowicz, S.M.; Wallin, K.F.; Raffa, K.F.; Harrison, R.G. Phylogeography of spruce beetles (*Dendroctonus rufipennis* Kirby) (Curculionidae: Scolytinae) in North America. *Mol. Ecol.* **2007**, *16*, 2560–2573.

38. Raffa, K.F.; Aukema, B.H.; Bentz, B.J.; Carroll, A.L.; Hicke, J.A.; Turner, M.G.; Romme, W.H. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience* **2008**, *58*, 510–517.

39. Kärvemo, S. *Population Dynamics of Tree-Killing Bark Beetles-a Comparison of the European Spruce Bark Beetle and the North American Mountain Pine Beetle. Introductory Research Essay, No. 10*; Swedish University of Agricultural Sciences, Department of Ecology: Uppsala, Sweden, 2010.

40. Dyer, E.D.A. Influence of temperature inversion on development of spruce beetle, *Dendroctonus obesus* (Mannerheim) (Coleoptera: Scolytidae). *J. Entomol. Soc. Br. Columbia* **1969**, *66*, 41–45.

41. Dyer, E.D.A. Larval diapause in *Dendroctonus obesus* (Mannerheim) (Coleoptera: Scolytidae). *J. Entomol. Soc. Br. Columbia* **1970**, *67*, 18–21.

42. Dyer, E.D.A.; Hall, P.M. Factors affecting larval diapause in *Dendroctonus rufipennis* (Mannerheim) (Coleoptera: Scolytidae). *Can. Entomol.* **1977**, *109*, 1485–1490.

43. Hansen, E.M.; Bentz, B.J.; Turner, D.L. The physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* **2001**, *133*, 805–817.

44. Hansen, E.M.; Bentz, B.J.; Powell, J.A.; Gray, D.R.; Vandygriff, J.C. Prepupal diapause and instar IV development rates of the spruce beetle, spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). *J. Insect Phys.* **2011**, *57*, 1347–1357.

45. Hansen, E.M.; Bentz, B.J. Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). *Can. Entomol.* **2003**, *135*, 697–712.

46. Safranyik, L.; Linton, D.A. Spruce beetle (Coleoptera: Scolytidae) survival in stumps and windfall. *Can. Entomol.* **1999**, *131*, 107–113.

47. Hansen, E.M.; Bentz, B.J.; Turner, D.L. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* **2001**, *133*, 827–841.

48. Logan, J.A.; Schmid, J.M.; Mehl, M.S. *A Computer Program to Calculate the Susceptibility of Spruce-Fir Stands to Spruce Beetle Outbreaks*; Research Note RM-393; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1980.

49. Wallin, K.F.; Raffa, K.F. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecol. Monogr.* **2004**, *74*, 101–116.

50. Massey, C.L.; Wygant, N.D. *Biology and Control of the Engelmann Spruce Beetle in Colorado*; Circular 944; USDA Forest Service: Washington, DC, USA, 1954; p. 35.

51. Miller, L.K.; Werner, R.A. Cold-Hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. *Can. J. Zoo.* **1987**, *65*, 2927–2930.

52. Rousseau, J.; Bauce, É.; Lavallée, R.; Guertin, C. Winter mortality and supercooling point of the spruce beetle (Coleoptera: Curculionidae) not affected by host tree vigor in Nova Scotia, Canada. *J. Acad. Entomol. Soc*. **2010**, *8*, 1–10.

53. Paine, T.D.; Raffa, K.F.; Harrington, T.C. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annu. Rev. Entomol.* **1997**, *42*, 179–206.

54. Cobb, F.W., Jr. Interactions among Root Disease Pathogens and Bark Beetles in Coniferous Forests. In Proceedings of the 7th International Conference on Root and Butt Rots, Vernon and Victoria, BC, Canada, 9–16 August 1988; Morrison, D.J., Ed., International Forestry Research Organizations: Victoria, BC, Canada: 1989; pp. 142–148.

55. James, R.L.; Goheen, D.L. Conifer mortality associated with root disease and insects in Colorado. *Plant Dis.* **1981**, *65*, 506–507.

56. McDonald, G.I. Preliminary Report on the Ecology of Armillaria in Utah and the Inland West. In Proceedings of the 46th Western International Forest Disease Work Conference, University of Nevada Campus, Reno, NV, USA, 28 September–2 October 1998; Trummer, L., Ed.; 1999; pp. 85–92.

57. Lewis, K.J.; Lindgren, S.B. Relationship between spruce beetle and tomentosus root disease: Two natural disturbance agents of spruce. *Can. J. For. Res.* **2002**, *32*, 31–37.

58. Hebertson, E.G.; Jenkins, M.J. The influence of fallen tree timing spruce beetle brood production. *West. N. Am. Nat.* **2007**, *67*, 452–460.

59. Schmid, J.M. *Spruce Beetles in Blowdown*; Resource Note RM-411; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1981.

60. Werner, R.A.; Holsten, E.H. Factors influencing generation times of spruce beetles in Alaska. *Can. J. For. Res.* **1985**, *15*, 438–443.

61. Kulakowski, D.; Veblen, T.T. Subalpine forest development following a blowdown in the Mount Zirkel Wilderness, Colorado. *J. Veg. Sci.* **2003**, *14*, 653–660.

62. Hard, J.S. Sequence of trees attacked by spruce beetles in a mature even-aged spruce stand in south-central Alaska. *Northwest Sci.* **1989**, *63*, 5–12.

63. Wood, S.L. The bark and ambrosia beetles (Coleoptera: Scolytidae) of North and Central America, a taxonomic monograph. *Gt. Basin Nat. Mem.* **1982**, *6*, 1–1359.

64. Byers, J.A. Wind-aided dispersal of simulated bark beetles flying through forests. *Ecol. Mod.* **2000**, *125*, 231–243.

65. Hard, J.S. Spruce beetles attack slowly growing spruce. *For. Sci.* **1985**, *31*, 839–850.

66. Berryman, A.A. Population Dynamics of Bark Beetles. In *Bark Beetles of North American Conifers*; Mitton, J.B., Sturgeon, K.B., Eds.; University of Texas Press: Austin, TX, USA, 1982; pp. 264–314.

67. DeRose, R.J.; Long, J.N. Factors influencing the spatial and temporal dynamics of Engelmann spruce mortality during a spruce beetle outbreak on the Markagunt Plateau, Utah. *For. Sci.* **2012**, *51*, 1–13.

68. Boone, C.A.; Aukema, B.H.; Bolmann, J.; Carroll, A.L.; Raffa, K.F. Efficacy of tree defense physiology varies with bark beetle population density: A basis for positive feedback in eruptive species. *Can. J. For. Res.* **2011**, *41*, 1174–1188.

69. Byers, J.A. Host Tree Chemistry Affecting Colonization in Bark Beetles. In *Chemical Ecology of Insects*, 2nd ed.; Cardé, R.T., Bell, W.J., Eds.; Chapman and Hall: New York, NY, USA, 1995; pp. 154–213.

70. Wallin, K.F.; Raffa, K.F. Influences of external chemical cues and internal physiological characteristics on the multiple steps of post-landing host selection behavior of *Ips pini* (Coleoptera: Scolytidae). *Environ. Entomol.* **2000**, *29*, 442–453.

71. Safranyik, L.; Linton, D.A. *Line Intersect Sampling for the Density and Bark Area of Logging Residue Susceptible to the Spruce Beetle, Dendroctonus rufipennis (Kirby)*; Information Report 1987, BC-X-295; Government of Canada, Canadian Forestry Service, Pacific Forestry Centre: Victoria, BC, Canada, 1987.

72. Raffa, K.F.; Berryman, A.A. The role of host plant resistance in the colonization behavior and ecology of bark beetles. *Ecol. Monogr.* **1983**, *53*, 27–49.

73. Moeck, H.A.; Wood, D.L.; Lindahl, K.Q., Jr. Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosae* with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. *J. Chem. Ecol.* **1981**, *7*, 49–83.

74. Cardoza, Y.J.; Moser, J.C.; Klepzig, K.D.; Raffa, K.F. Multipartite symbioses among fungi, mites, nematodes, and the spruce beetle, *Dendroctonus rufipennis*. *Environ. Entomol.* **2008**, *37*, 956–963.

75. Adams, A.S.; Currie, C.R.; Cardoza, Y.; Klepzig, K.D.; Raffa, K.F. Effects of symbiotic bacteria and tree chemistry on the growth and reproduction of bark beetle fungi symbionts. *Can. J. For. Res.* **2009**, *39*, 1133–1147.

76. Cardoza, Y.J.; Klepzig, K.D.; Raffa, K.F. Bacteria in oral secretions of an endophytic insect inhibit antagonistic fungi. *Ecol. Entomol.* **2006**, *31*, 636–645.

77. Six, D.L.; Bentz, B.J. Fungi associated with the North American spruce beetle, *Dendroctonus rufipennis*. *Can. J. For. Res.* **2003**, *33*, 1815–1820.

78. Solheim, H. A Comparison of Blue-Stain Fungi Associated with the North American Spruce Beetle *Dendroctonus rufipennis* and the Eurasian Spruce Bark Beetle *Ips typographus*. In Proceedings of the Forest Pathology Research in the Nordic Countries, SNS Conference, Biri, Norway, 9–12 August 1994; Amlid, D., Ed.; Norsk Institutt for Skorgforskning: As, Norway, 1995; pp. 61–67.

79. Hinds, T.E.; Buffan, P.E. *Blue Stain in Engelmann Spruce Trap Trees Treated with Cacodylic Acid*; Research Note RM-201; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1971.

80. Bentz, B.J.; Six, D.L. Ergosterol content of fungi associated with *Dendroctonous ponderosae* and *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). *Entomol. Soc. Am.* **2006**, *99*, 189–194.

81. Klepzig, K.D.; Six, D.L. Bark beetle-fungal symbiosis: Context dependency in complex associations. *Symbiosis* **2004**, *37*, 189–205.

82. Aukema, B.H.; Werner, R.A.; Haberkern, K.E.; Illman, B.L.; Clayton, M.K.; Raffa, K.F. Quantifying sources of variation in the frequency of fungi associated with spruce beetles: Implications for hypothesis testing and sampling methodology in bark beetle-symbiont relationships. *For. Ecol. Manag.* **2005**, *217*, 187–202.

83. Reynolds, K.M. Relations between activity of *Dendroctonus rufipennis* Kirby on Lutz spruce and blue stain associate *Leptographium abietinum* (Peck) Wingfield. *For. Ecol. Manag.* **1992**, *47*, 71–86.

84. Safranyik, L.; Shrimpton, D.M.; Whitney, H.S. The Role of Host-Pest Interaction in Population Dynamics of *Dendroctonus rufipennis* Kirby (Coleoptera: Scolytidae). In Proceedings of the IUFRO/MAB Symposium, Host-Pest Interactions, Irkutsk, USSR, 24–27 August 1981; Isaev, A.S., Ed.; Candian Forest Service: Victoria, BC, Canada, 1981; pp. 1–12.

85. Ohsawa, M.; Langor, D.; Hiratsuka, L.; Yamaoka, Y. Fungi associated with *Dendroctonus rufipennis* and *Polygraphus rufipennis*, and white spruce inoculation tests. *Can. J. Plant Pathol* **2000**, *22*, 254–257.

86. Cardoza, Y.J.; Paskewitz, S.; Raffa, K.F. Travelling through time and space on the wings of beetles: A tripartite insect-fungi-nematode association. *Symbiosis J.* **2006**, *41*, 71–79.

87. Gara, R.I.; Werner, R.A.; Whitmore, M.C.; Holsten, E.H. Arthropod associates of the spruce beetle *Dendroctonus rufipennis* (Kirby) (Coleoptera: Scolytidae) in spruce stands of south-central and interior Alaska. *J. Appl. Entomol.* **1995**, *119*, 585–590.

88. Fayt, P.; Machmer, M.M.; Steeger, C. Regulation of spruce bark beetles by woodpeckers—A literature review. *For. Ecol. Manag.* **2005**, *206*, 1–14.

89. Pretzlaw, T.; Trudeau, C.; Humphries, M.M.; LaMontagne, J.M.; Boutin, S. Red squirrels (*Tamiasciurus hudsonicus*) feeding on spruce bark beetles (*Dendroctonus rufipennis*): Energetic and ecological implications. *J. Mammal.* **2006**, *87*, 909–914.

90. Reynolds, K.M.; Holsten, E.H. The relative importance of risk factors for spruce beetle outbreaks. *Can. J. For. Res.* **1994**, *24*, 2089–2095.

91. Chapman, T.B.; Veblen, T.T.; Schoennagel, T. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* **2012**, *93*, 2175–2185.

92. Mattson, W.J.; Haack, R.A. The role of drought in outbreaks of plant-eating insects: Drought's physiological effects on plants can predict its influence on insect populations. *BioScience* **1987**, *37*, 110–118.

93. Kausrud, K.; Okland, B.; Skarpaas, O.; Grégoire, J.C.; Erbilgin, N.; Stenseth, N.C. Population dynamics in changing environments: The case of an eruptive forest pest species. *Biol. Rev. Camb. Philos. Soc.* **2012**, *87*, 34–51.

94. Chapman, T.B.; Veblen, T.T.; Schoennagel, T. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* **2012**, *93*, 10, 2175–2185.

95. DeRose, R.J.; Bentz, B.J.; Long, J.N.; Shaw, J.D. Effect of increasing temperatures on the distribution of spruce beetle in Engelmann spruce forests of the Interior West, USA. *For. Ecol. Manag.* **2013**, *308*, 198–206.

96. DeRose, R.J.; Long, J.N. Wildfire and spruce beetle outbreak: Simulation of interacting disturbances in the central Rocky Mountains. *Ecoscience* **2009**, *16*, 28–38.

97. Edmonds, R.L.; Agee, J.K.; Gara, R.I. *Forest Health and Protection*; McGraw Hill: New York, NY, USA, 2000; p. 630.

98. Agee, J.K. *Fire Ecology of Pacific Northwest Forests*; Island Press: Washington, DC, USA, 1993; p. 493.

99. Buechling, A.; Baker, W.L. A fire history from tree rings in a high-elevation forest of Rocky Mountain National Park. *Can. J. For. Res.* **2004**, *34*, 1259–1273.

100. Alexander, R.R. *Ecology, Silviculture, and Management of the Engelmann Spruce-Subalpine Fir Type in the Central and Southern Rocky Mountains*; Agriculture Handbook No. 659; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1987.

101. Jenkins, M.J.; Dicus, C.A.; Hebertson, E.G. Post-Fire Succession and Disturbance Interactions on an Intermountain Subalpine Spruce-Fir Forest. In *Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription*, Proceedings of the 20th Tall Timbers Fire Ecology Conference, Tall Timbers Research Station, Tallahassee, FL, USA, 7–10 May 1998; Pruden, T.L., Brennan, L.A., Eds.; Volume 459, pp. 219–229.

102. Baker, W.L.; Veblen, T.T. Spruce beetles and fires in the nineteenth-century subalpine forests of western Colorado. *Arct. Alp. Res.* **1990**, *22*, 65–80.

103. Wright, H.A.; Bailey, A.W. *Fire Ecology: United States and Southern Canada*; John Wiley and Sons: New York, NY, USA, 1982; pp. 125–135.

104. Hopkins, A.D. *Practical Information on the Scolytid Beetles of North American Forests: Bark Beetles of the Genus Dendroctonus*; Part I: Bulletin 83; United States Bureau of Entomology: Washington, DC, USA, 1909; pp. 126–132.

105. Jenkins, M.J.; Page, W.G.; Hebertson, E.G.; Alexander, M.E. Fuels and fire behavior dynamics in bark beetle attacked forests in western North America and implications for fire management. *For. Ecol. Manag.* **2012**, *275*, 23–34.

106. Jenkins, M.J.; Hebertson, E.G.; Page, W.G.; Jorgensen, C.A. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *For. Ecol. Manag.* **2008**, *254*, 16–34.

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

108. Page, W.G.; Jenkins, M.J.; Runyon, J.B. Spruce beetle-induced changes to Engelmann spruce foliage flammability. *For. Sci.* **2014**, in press.

109. Jorgensen, C.A.; Jenkins, M.J. Fuel complex alterations associated with spruce beetle-induced tree mortality in Intermountain spruce-fir forests. *For. Sci.* **2011**, *57*, 232–240.

110. Page, W.G.; Jenkins, M.J. Mountain pine beetle induced changes to selected lodgepole pine fuel complexes within the Intermountain Region. *For. Sci.* **2007**, *53*, 507–518.

111. Klutsch, J.G.; Negron, J.F.; Costello, S.L.; Rhoades, C.C.; West, D.R.; Popp, J.; Caissie, R. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *For. Ecol. Manag.* **2009**, *258*, 641–649.

112. Simard, M.; Romme, W.H.; Griffin, J.M.; Turner, M.G. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecol. Monogr.* **2011**, *81*, 3–24.

113. Jenkins, M.J. Fuel and Fire Behavior in High Elevation Five-Needle Pines Affected by Mountain Pine Beetle. In *The Future of High-Elevation, Five-Needle White Pines in Western North America*, Proceedings of the High Five Symposium, Missoula, MT, USA, 28–30 June 2010; Keane, R.E., Tomback, D.F., Murray, M.P., Smith, C.M., Eds.; US Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2011; RMRS-P-63, Volume 376, pp. 190–197.

114. Toone, C.L.; Jenkins, M.J. Influence of mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae: Scolytinae) on fuels, foliar fuel moisture content, and litter and volatile terpenes in whitebark pine (*Pinus albicaulis*). *Forests* **2014**, submitted.

115. Donato, D.C.; Harvey, B.; Romme, W.H.; Simard, M.; Turner, M.G. Bark beetle effects of fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. *Ecol. Soc. Am.* **2013**, *23*, 3–20.

116. McMillin, J.D.; Allen, K.K. Effects of Douglas-fir beetle (Coleoptera: Scolytidae) infestations on forest overstory and understory conditions in western Wyoming. *West. N. Am. Nat.* **2003**, *63*, 498–506.

117. Harvey, B.J.; Donato, D.C.; Romme, W.H.; Turner, M.G. Influence of recent bark beetle outbreak on fire severity and post-fire regeneration in montane Douglas-fir forests. *Ecology* **2013**, *94*, 2475–2486.

118. Bigler, C.; Veblen, T.T. Changes in litter and dead wood loads following tree death beneath subalpine conifer species in northern Colorado. *Can. J. For. Res.* **2011**, *41*, 331–340l.

119. Mielke, J.L. Rate of deterioration of beetle-killed Engelmann spruce. *J. For.* **1950**, *48*, 882–889.

120. Schmid, J.M.; Hinds, T.E. *Development of Spruce-Fir Stands Following Spruce Beetle Outbreaks*; Research Paper RM-131; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1974; p. 16.

121. Bigler, C.; Kulakowski, D.; Veblen, T.T. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. *Ecology* **2005**, *86*, 3018–3029.

122. Kulakowski, D.; Veblen, T.T. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* **2007**, *88*, 759–769.

123. Schulz, B. *Changes in Downed and Dead Woody Material Following a Spruce Beetle Outbreak on the Kenai Peninsula, Alaska*; Research Paper PNW-RP-559; USDA Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 2003; p. 10.

124. Rothermel, R.C. *How to Predict the Spread and Intensity of Forest and Range Fires*; General Technical Report INT-GTR-143; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1983; p. 161.

125. Albini, F.A.; Baughman, R.G. *Estimating Windspeeds for Predicting Wildland Fire Behavior*; Research Paper INT-221; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1979.

126. Byram, G.M.; Jemison, G.M. Solar radiation and forest fuel moisture. *J. Agric. Res.* **1943**, *67*, 149–176.

127. Rothermel, R.C.; Wilson, R.A., Jr.; Morris, G.A.; Sackett, S.S. *Modeling Moisture Content of Fine Dead Wildland Fuels: Input to the BEHAVE Fire Prediction System*; Research Paper INT-359; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1986; p. 61.

128. Rothermel, R.C. *A Mathematical Model for Predicting Fire Spread in Wildland Fuels*; Research Paper INT-115, USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1972; p. 40.

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

130. Sandberg, D.V.; Riccardi, C.L.; Schaaf, M.D. Reformulation of Rothermel's wildland fire behavior model for heterogeneous fuelbeds. *Can. J. For. Res.* **2007**, *37*, 2438–2455.

131. Schroeder, M.; Buck, C.C. *Fire Weather*; Agriculture Handbook 360; USDA Forest Service: Washington, DC, USA, 1970.

132. Albini, F.A.; Brown, J.K. *Predicting Slash Depth for Fire Modeling*; Research Paper INT-221; USDA Forest Service, Intermountain Forest and Range Experiment Station: Odgen, UT, USA, 1978; p. 24.

133. 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*, 1–14.

134. Van Wagner, C.E. Conditions for the start and spread of crown fire. *Can. J. For. Res.* **1977**, *7*, 23–34.

135. Bessie, W.C.; Johnson, E.A. The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* **1995**, *76*, 747–762.

136. Susott, R.A. *Effect of Heating Rate on Char Yield from Forest Fuels*; Research Note INT-295; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1980; p. 9.

137. Alexander, M.E.; Cruz, M.G. Evaluating a model for predicting active crown fire rate of spread using wildfire observations. *Can. J. For. Res.* **2006**, *36*, 3015–3028.

138. Cruz, M.G.; Alexander, M.E. Assessing crown fire potential in coniferous forests of western North America: A critique of current approaches and recent simulation studies. *Int. J. Wildland Fire* **2010**, *19*, 377–398.

139. Alexander, M.E.; Cruz, M.G. Are the applications of wildland fire behavior models getting ahead of their evaluation again? *Environ. Model. Softw.* **2013**, *41*, 65–71.

140. Knight, D.H. Parasites, Lightning, and the Vegetation Mosaic in Wilderness Landscapes. In *Landscape Heterogeneity and Disturbance*; Turner, M.G., Ed.; Springer-Verlag: New York, NY, USA, 1987; pp. 59–83.

141. Page, W.G.; Alexander, M.E.; Jenkins, M.J. Wildfire's resistance to control in mountain pine beetle-attacked lodgepole pine forests. *For. Chron.* **2013**, *89*, 43–54.

142. Samman, S.; Logan, J. *Assessment and Response to Bark Beetle Outbreaks in the Rocky Mountain Area*; General Technical Report, RMRS-GTR-62; USDA Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2000.

143. Goyer, R.A.; Wagner, M.R.; Schowalter, T.D. Current and Proposed Technologies for bark beetle management. *J. For.* **1998**, *96*, 29–33.

144. Maser, C.; Trappe, J.M. *The Seen and Unseen World of the Fallen Tree*; General Technical Report PNW-164; USDA Forest Service, Pacific Northwest Forest and Range Experiment Station: Portland, OR, USA, 1984.

145. Graham, R.L.; Cromack, K., Jr. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.* **1982**, *12*, 511–521.

146. Holsten, E.H.; Their, R.W.; Munson, A.S.; Gibson, K.E. *The Spruce Beetle*; Insect & Disease Leaflet No. 127; USDA Forest Service: Washington, DC, USA, 1999; p. 12.

147. Helm, A.C.; Johnson, J.E. *A Handbook for Forest Vegetation Management in Recreation and Historic Parks*; Publication 420–143; Virginia Cooperative Extension, Virginia Polytechnic Institute and State University: Blacksburg, VA, USA, 1995.

148. Veblen, T.T.; Hadley, K.S.; Reid, M.S.; Rebertus, A.J. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* **1991**, *72*, 213–231.

149. Aplet, G.H.; Laven, R.D.; Smith, F.W. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. *Ecology* **1988**, *69*, 312–319.

150. Peet, R.K. Forests of the Rocky Mountains. In *North American Terrestrial Vegetation*; Barbour, M.G., Billlings, W.D., Eds.; Cambridge University Press: New York, NY, USA, 1988.

151. Schmid, J.M.; Mata, S.A. *Natural Variability of Specific Forest Insect Populations and Their Associated Effects in Colorado*; General Technical Report RM-GTR-275; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1996; p. 14.

152. Wilford, B.H. *Engelmann Spruce Beetle Surveys*; Review Draft of Proposed Manual, Copy on File at USDA Forest Service; Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1965; p. 121.

153. Meddens, A.J.H.; Hicke, J.A.; Vierling, L.A.; Hudak, A.T. Evaluating methods to detect bark beetle caused tree mortality using single-date and multi-date Landsat imagery. *Remote Sens. Environ.* **2013**, *132*, 49–58.

154. Johnson, J.; Greenfield, P.; Munson, A.S. An Evaluation of the Utility of Sub-Pixel Analysis of Thematic Mapper Imagery for the Spruce Beetle Outbreak on the Manti-LaSal National Forest. In *Natural Resource Management Using Remote Sensing and GIS*, Proceedings of the Seventh Forest Service Remote Sensing Applications Conference, Nassau Bay, TX, USA, 6–10 April 1998; Greer, J.D., Ed.; pp. 276–287.

155. Morris, A.; Baker, M., Jr. Aerial Sketchmapping and GIS within the US Forest Service. In Proceedings of the Integrating GIS with Other Technologies, Esri International User Conference, San Diego, CA, USA, 9–13 July 2001. Available online: http://proceedings.esri.com/library/userconf/proc01/professional/ (accessed on 28 October 2013).

156. Knight, F.B. Measurement of Engelmann spruce beetle populations. *Ecology* **1960**, *41*, 249–252.

157. Hansen, E.M.; Vandygriff, J.C.; Cain, R.J.; Wakarchuk, D. Comparison of naturally and synthetically baited spruce beetle trapping systems in the central Rocky Mountains. *J. Econ. Entomol.* **2006**, *99*, 373–382.

158. Bentz, B.J. *Forest Insect and Disease Tally System (FINDIT) User Manual*; General Technical Report RMRS-GTR-49; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 2000.

159. Bentz, B.J.; Amman, G.D.; Logan, J.A. Critical assessment of risk classification systems for the mountain pine beetle. *For. Ecol. Manag.* **1993**, *61*, 349–366.

160. Shore, T.L.; Safranyik, L.; Lemieux, J. Susceptibility of lodgepole pine stands to the mountain pine beetle: Testing of a rating system. *Can. J. For. Res.* **2000**, *30*, 44–49.

161. Schmid, J.M.; Frye, R.H. *Stand Ratings for Spruce Beetles*; Research Note RM-309; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1976; p. 4.

162. Steele, R.; Williams, R.E.; Weatherby, J.C.; Reinhardt, E.D.; Hoffman, J.T.; Thier, R.W. *Stand Hazard Rating for Central Idaho Forests*; General Technical Report INT-GTR-332; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1996; p. 29.

163. Hansen, E.M.; Negron, J.F.; Munson, A.S.; Anhold, J.A. A retrospective assessment of partial cutting to reduce spruce beetle-caused mortality in the Southern Rocky Mountains. *West. J. Appl. For.* **2010**, *25*, 81–87.

164. Long, J.N. A practical approach to density management. *For. Chron.* **1985**, *61*, 23–27.

165. Schmitt, C.L.; Powell, D.C. *Rating Forest Stands for Insect and Disease Susceptibility: A Simplified Approach, Version 2.0*; BMPMSC-05-01; USDA Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest, Blue Mountains Pest Management Service Center: La Grande, OR, USA, 2005; p. 20.

166. Daniel, T.W.; Helms, J.A.; Baker, F.S. *Principles of Silviculture*, 2nd ed.; McGraw-Hill: New York, NY, USA, 1979; p. 500.

167. Bartos, D.L.; Amman, G.D. *Microclimate: An Alternative to Tree Vigor as a Basis for Mountain Pine Beetle Infestations*; Research Paper INT-400; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1989.

168. Schowalter, T.D.; Caldwell, B.A.; Carpenter, S.E.; Griffiths, R.P.; Harmon, E.R.; Ingram, E.R.; Kelsey, R.G.; Lattin, J.D.; Moldenke, A.R. Decomposition of Fallen Trees: Effects of Initial Conditions and Heterotroph Colonization Rates. In *Tropical Ecosystems; Ecology and Management*; Singh, K.P., Singh, J.S., Eds.; Wiley Eastern Ltd.: New Delhi, India, 1992; pp. 373–383.

169. Amman, G.D.; McGregor, M.D.; Schmitz, R.F.; Oakes, R.D. Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands. *Can. J. For. Res.* **1988**, *18*, 688–695.

170. Sartwell, C.; Stevens, R.E. Mountain pine beetle in ponderosa pine-prospects for silvicultural control in second-growth stands. *J. For.* **1975**, *73*, 136–140.

171. Alexander, R.R. *Silvicultural Systems and Cutting Methods for Old-Growth Spruce-Fir Forests in the Central and Southern Rocky Mountains*; General Technical Report RM-126; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1987.

172. Shaw, J.D. Application of stand density index to irregularly structured stands. *West. J. Appl. For.* **2000**, *15*, 40–42.

173. DeRose, R.J.; Long, J.N. Regeneration response and seedling bank dynamics on a *Dendroctonus rufipennis*-killed *Picea engelmannii* landscape. *J. Veg. Sci.* **2010**, *21*, 377–387.

174. Schmid, J.M. *Guidelines for Minimizing Spruce Beetle Populations in Logging Residuals*; Research Paper RM-185; USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1977; p. 8.

175. Bentz, B.J.; Munson, A.S. Spruce beetle population suppression in northern Utah. *West. J. Appl. For.* **2000**, *15*, 122–128.

176. Alexander, R.R. *Partial Cutting in Old Growth Spruce-Fir*; Research Paper RM-110; USDA Forest Service, Rocky Mtn. Forest & Range Exp. Station: Fort Collins, CO, USA, 1973; p. 16.

177. Kile, G.A.; McDonald, G.I.; Byler, J.W. Ecology and Disease in Natural Forests. In *Armillaria Root Disease, Agricultural Handbook 691*; Shaw, C.G., Kile, G.A., Eds.; USDA Forest Service: Washington, DC, USA, 1991; pp. 102–121.

178. Munson, A.S.; Steed, B.; Fettig, C.J. *Using Insecticides to Protect Individual Conifers from Bark Beetle Attack in the West*; USDA Forest Service, Intermountain and Northern Regions, Forest Health Protection: Ogden, UT, USA, 2011.

179. Fettig, C.J.; Munson, A.S.; McKelvey, S.R.; Bush, P.B.; Borys, R.R. Spray deposition from ground-based applications of carbaryl to protect individual trees from bark beetle attack. *J. Environ. Qual.* **2008**, *37*, 1170–1179.

180. Fettig, C.J.; Allen, K.K.; Borys, R.R.; Christopherson, J.; Dabney, C.P.; Eager, T.A.; Gibson, K.E.; Hebertson, E.G.; Long, D.F.; Munson, A.S.; *et al.* Effectiveness of bifenthrin (Onyx™) and carbaryl (Sevin® SL) for protecting individual, high-value trees from bark beetle attack (Coleoptera: Curculionidae, Scolytinae) in the western United States. *J. Econ. Entomol.* **2006**, *99*, 1691–1698.

181. Fettig, C.J.; Grosman, D.M.; Munson, A.S. Advances in Insecticide Tools and Tactics for Protecting Conifers from Bark Beetle Attack in the Western United States. In *Insecticides—Development of Safer and More Effective Technologies*; Trdan, S., Ed.; InTech: Rijeka, Croatia, 2013; pp. 472–492.

182. Hastings, F.L.; Holsten, E.H.; Shea, P.J.; Werner, R.A. Carbaryl: A review of its use against bark beetles in coniferous forests of North America. *Environ. Entomol.* **2001**, *30*, 803–810.

183. Johnson, K.J. Effectiveness of Carbaryl and Pyrethroid Insecticides for Protection of Engelmann Spruce from Attack by Spruce Beetle (Coleoptera: Scolytidae). Master's Thesis, Utah State University, Logan, UT, USA, 1996.

184. Shea, P.J.; Holsten, E.H.; Hard, J. Bole implantation of systemic insecticides does not protect trees from spruce beetle attack. *West. J. Appl. For.* **1991**, *6*, 4–7.

185. Grosman, D.M.; Fettig, C.J.; Jorgensen, C.L.; Munson, A.S. Effectiveness of two systemic insecticides for protecting western conifers from mortality due to bark beetle attack. *West J. Appl. For.* **2010**, *25*, 181–185.

186. Borden, J.H. Disruption of Semiochemical-Mediated Aggregation in Bark Beetles. In *Insect Pheromone Research: New Directions*; Cardé, R.T., Minks, A.K., Eds.; Chapman and Hall: New York, NY, USA, 1997; pp. 421–438.

187. Skillen, E.L.; Berisford, C.W.; Camann, M.A.; Reardon, R.C. *Semiochemicals of Forest and Shade Tree Insects in North America and Management Applications*; FHTET-96-15; USDA Forest Service, Forest Health Technology Enterprise Team: Morgantown, WV, USA, 1997; p. 182.

188. Shea, P.J. *Proceedings of the Symposium on Management of Western Bark Beetles with Pheromones: Research and Development*; General Technical Report PSW-GTR-150; USDA Forest Service, Pacific Southwest Research Station: Albany, CA, USA, 1992; p. 53.

189. Wood, D.L.; Stark, R.W.; Waters, W.W.; Bedard, W.D.; Cobb, F.W., Jr. Treatment Tactics and Strategies. In *Integrated Pest Management in Pine-Bark Beetle Ecosystems*; Waters, W.W., Stark, R.W., Wood, D.L., Eds.; John Wiley and Sons: New York, NY, USA, 1985; pp. 121–140.

190. Silverstein, R.M.; Brownlee, R.G.; Bellas, T.E.; Wood, D.L.; Browne, L.E. Brevicomin: Principal sex attractant in the frass of the female western pine beetle. *Science* **1968**, *158*, 889–891.

191. Borden, J.H. Semiochemicals and bark beetle populations: Exploitation of natural phenomena by pest management strategists. *Ecography* **2006**, *12*, 501–510.

192. Furniss, M.M.; Orr, P.W. *Douglas fir Beetle*. *Insect & Disease Leaflet*, No 5; USDA Forest Service: Washington, DC, USA, 1978; p. 7.

193. Rudinsky, J.A.; Morgan, M.E.; Linsey, L.M.; Putman, T.B. Additional components of the Douglas-fir beetle (Col., Scolytidae) aggregative pheromone and their possible utility in pest control. *Zeitschrift fuer Angew. Entomol.* **1974**, *76*, 65–77.

194. Lindgren, B.S.; McGregor, M.D.; Oakes, R.D.; Meyer, H.E. Suppression of spruce beetle attacks by MCH released from bubble caps. *West. J. Appl. For.* **1989**, *4*, 49–52.

195. Dyer, E.D.A.; Hall, P.M. Effect of anti-aggregative pheromones 3,2-MCH and trans-verbenol on *Dendroctonus rufipennis* attacks on spruce stumps. *J. Entomol. Soc. Br. Columbia* **1977**, *74*, 32–34.

196. Furniss, M.M.; Baker, B.H.; Hostetler, B.B. Aggregation of spruce beetles (Coleoptera) to seudenol and repression of attraction by methylcyclohexenone in Alaska. *Can. Entomol.* **1976**, *108*, 1297–1302.

197. Kline, L.N.; Schmitz, R.F.; Rudinsky, J.A.; Furniss, M.M. Repression of spruce beetle (Coleoptera) attraction by methylcyclohexenone in Idaho. *Can. Entomol.* **1974**, *106*, 485–491.

198. Werner, R.A.; Holsten, E.H. Current Status of Research with the Spruce Beetle, *Dendroctonus rufipennis*. In *Application of Semiochemicals for Management of Bark Beetle Infestations*, Proceedings of an Informal Conference, Salom, S.M., Hobson, K.R., Eds.; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1985; INT-GTR-318, pp. 23–29.

199. Holsten, E.H.; Shea, P.J.; Borys, R.R. MCH released in a novel pheromone dispenser prevents spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Scolytidae), attacks in south-central Alaska. *J. Econ. Entomol.* **2003**, *96*, 31–34.

200. Ross, D.W.; Daterman, G.E.; Munson, A.S. Evaluation of the anti-aggregation pheromone, 3-methylcyclohex-2-en-1-one (MCH), to protect live spruce from spruce beetle (Coleoptera: Scolytidae) infestation in southern Utah. *J. Entomol. Soc. Br. Columbia* **2004**, *101*, 145–146.

201. Ross, D.W.; Gibson, K.E.; Daterman, G.E. *Using MCH to Protect Trees and Stands from Douglas-Fir Beetle Infestation*; FHTET-2001-09; USDA Forest Service, Forest Health Technology Enterprise Team: Morgantown, WV, USA, 2001.

202. Poland, T.M.; Borden, J.H.; Stock, A.J.; Chong, L.J. Green leaf volatiles disrupt responses by the spruce beetle, *Dendroctonus rufipennis*, and the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae) to attractant-baited traps. *J. Entomol. Soc. Br. Columbia* **1998**, *95*, 17–24.

203. Werner, R.A.; Hard, J.; Holsten, E.H. The development of management strategies to reduce the impact of the spruce beetle in south-central Alaska. *Northwest Environ. J.* **1988**, *4*, 319–358.

204. Poland, T.M.; Borden, J.H. Disruption of secondary attraction of the spruce beetle, *Dendroctonus rufipennis*, by pheromones of two sympatric species. *J. Chem. Ecol.* **1997**, *24*, 151–166.

205. Ross, D.W.; Daterman, G.E.; Munson, A.S. Spruce beetle (Coleoptera: Scolytidae) response to traps baited with selected semiochemicals in Utah. *West. N. Am. Nat.* **2005**, *65*, 123–126.

206. Lindgren, B.S. A multiple funnel trap for scolytid beetles (Coleoptera). *Can. Entomol.* **1983**, *115*, 299–302.

207. Nagel, R.H.; McComb, D.; Knight, F.B. Trap tree method for controlling the Engelmann spruce beetle in Colorado. *J. For.* **1957**, *55*, 894–898.

208. Wygant, N.D. Use of Trap Trees for Suppression. In Proceedings of the Conference on Engelmann Spruce Beetle Surveys and Suppression, Ogden, UT, USA, 1960; p. 3.

209. Dyer, E.D.A.; Safranyik, L. Assessment of pheromone-baited trees on spruce beetle population (Coleoptera; Scolytidae). *Can. Entomol.* **1977**, *109*, 77–80.

210. Gray, D.R.; Holsten, E.H.; Pascuzzo, M. Effects of semiochemical baiting on the attractiveness of felled and unfelled lethal trap trees for spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Scolytidae), management in areas of high and low beetle populations. *Can. Entomol.* **1990**, *122*, 373–379.

211. Log Wizard^TM. Available online: http://www.logwizard.com/ (accessed on 4 November 2013).

212. Flint, C.G.; McFarlane, B.; Miller, M. Human dimensions of forest disturbance by insects: An international synthesis. *Environ. Manag.* **2009**, *43*, 1174–1186.

213. Jones, J. *Report on Insect Survey, Sevier Division, Dixie National Forest, Fall 1937, Cedar City, UT*; USDA Forest Service, Intermountain Region, Forest Health Protection, Ogden Field Office: Ogden, UT, USA, 1937.

214. Furniss, R.L. *Memorandum on Forest Insects on the Dixie National Forest, Utah, September 1940. Bureau of Entomology and Plant Quarantine*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1940.

215. Rice, W. *Annual Insect Report, R4, 1944*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1944.

216. Intermountain Region. *Engelmann Spruce Bark Beetle Infestation: Wasatch and Duchesne Counties, Utah-Ashley, Uinta and Wasatch National Forests*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1960.

217. Osmond, E.C.; Morgan, R.E.; Knopf, J.A.E. *Spring Narrative Accomplishment Report, Bridger National Forest, Insect Control Project, Green River Ranger District*; USDA Forest Service, Intermoutain Region: Ogden, UT, USA, 1962.

218. Washburn, R.I.; Knopf, J.A.E. *Engelmann Spruce Beetle Conditions: Uinta, Ashley, Wasatch National Forests, Appraisal Survey*; Forest Insect Research Report M-5123; USDA Forest Service, Intermountain Forest Range Experiment Station, Division of Forest Insect Research Report: Ogden, UT, USA, 1958.

219. Knopf, J.A.E. *Engelmann Spruce Conditions*; Forest Pest Management Report R-4, 5230; USDA Forest Service, Branch of Forest Insect and Disease Prevention and Control, Division of Timber Management, Intermountain Region: Ogden, UT, USA, 1962.

220. Klein, W.H. *Forest Insect Conditions on the Fishlake National Forest, 1967*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1967.

221. Parker, D.L. *A Biological Evaluation of Engelmann Spruce Beetle in Engelmann Spruce, Ephraim and Castle Dale Ranger Districts, Manti-La Sal National Forest*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1973.

222. Klein, W.H. *Engelmann Spruce Beetle Infestations, Fishlake National Forest, Region Four, Utah, 1971*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1971.

223. Holland, D.G. *Biological Evaluation of Spruce Beetle in Mill Hollow, Heber Ranger District, Uinta National Forest, 1981*; Forest Pest Management Report R-4, 83-4; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1983.

224. Holland, D.G. *Summary of Insect and Disease Conditions, 1980–1989, Bridger-Teton National Forest*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1990.

225. Knopf, J.A.E. *Forest Insect and Disease Conditions in the Intermountain Region during 1980*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1981.

226. Knapp, K. *Forest Insect and Disease Conditions in the Intermountain Region during 1984*; Forest Pest Management Report R4-INF; USDA Forest Service, Intermountain Region, Forest Insect Laboratory: Fort Collins, CO, USA, 1985.

227. Munson, A.S. *A Biological Evaluation of Spruce Beetle Activity within the South Manti Project Area, Manti-Lasal National Forest, Ferron Ranger District*; Forest Health Protection Report R4-94-05; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1994.

228. DeBlander, V.; Hansen, D. *Geyser Pass Spruce Beetle Survey, Manti-La Sal National Forest*; Forest Health Protection Report R4-94-07; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1994.

229. Munson, A.S.; DeBlander, V. *A Biological Evaluationof Spruce Beetle Activity on Midway Face, DixieNational Forest, Cedar RD, 1992*; Forest Pest Management Report R4-92-03; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1992.

230. LaMadeleine, L. *Review of Forest Pest Management Aerial Detection Survey for 1992*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1993.

231. Anhold, J.; DeBlander, V.; Hansen, D. *A Biological Evaluation of Spruce Beetle Activity in the Neff's Management Area, Fishlake National Forest, Loa RD, 1992*; Forest Pest Management Report R4-93-01; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1992.

232. Munson, A.S.; Anhold, J.; DeBlander, V. *A Biological Evaluation of Spruce Beetle in the Timber Canyon Management Unit, Manti-Lasal National, Sanpete Ranger District*. Forest Health Protection Report R4-92-04; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1992.

233. Hansen, D. *Review of Forest Health Protection 1995 Aerial Detection Survey, Ashley National Forest*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1995.

234. Anhold, J.; Hansen, D. *A Biological Evaluation of Spruce Beetle within the La Sal Pass Area, Manti-La Sal National Forest, Moab Ranger District*; Forest Health Protection Report R4-1998-01; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2000.

235. Anhold, J. *A Review of Forest Health Protection Aerial Detection Surveys, Wasatch-Cache National Forest, Kamas Ranger District*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1996.

236. Hebertson, E.G. *A Biological Evaluation of Spruce Beetle Activity in Coyote Gulch, Dixie National Forest, Escalante Ranger District*; Forest Health Protection Report R4-2000-02; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2000.

237. Anhold, J.; Dymerski, A. *Biological Evaluation of Spruce Beetle along the Monte Cristo Ridge, Wasatch-Cache National Forest*; Forest Health Protection Report R4-2000-001; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2000.

238. Hansen, D. *Summary of Spruce Beetle Activity in Bear Hodges Analysis Area, Wasatch-Cache National Forest, Logan Ranger District*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1997.

239. Munson, A.S. *Summary of the South Tent Analysis Area, Sanpete Ranger District, Manti-Lasal National Forest*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 1996.

240. Hebertson, E.G. *A Biological Evaluation of Spruce Beetle Activity in the Indian Creek Drainage, Moab-Monticello Watershed Improvement Project, Manti-La Sal National Forest, Moab-Monticello Ranger District*; Forest Health Protection Report R14-2002-03; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2002.

241. Anhold, J. *Biological Evaluation of Spruce Beetle in the Abajo Mountains, Monticello Ranger District, Manti-La Sal National Forest*; Forest Health Protection Report R4-2000-001; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2000.

242. Hebertson, E.G. *A Biological Evaluation of Spruce Beetle Activity in the South Fork of the Beaver River Watershed, Fishlake National Forest, Beaver Ranger District*; Forest Health Protection Report R14-2002-02; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2002.

243. Hebertson, E.G. *A Biological Evaluation of Spruce Beetle Activity on Barney Top, Dixie National Forest, Escalante Ranger District*; Forest Health Protection Report OFO-BE-03-001; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2003.

244. Hebertson, E.G. *Fremont River Watershed Assessment Project, Fishlake National Forest, Fremont Ranger District*; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2003.

245. Pederson, L.A. *A Biological Evaluation of Spruce Beetle Activity in the Lake Project Planning Area, Sanpete and Price Ranger Districts, Manti-La Sal National Forest*; Forest Health Protection Report OFO-PUB-04-001; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2004.

246. Hebertson, E.G. *A Biological Evaluation of Spruce Beetle Activity in Bryant's Fork, Uinta National Forest, Heber Ranger District*; Forest Health Protection Report R14–2004-02, USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2004.

247. Hebertson, E.G. *A Biological Evaluation of Spruce Beetle Activity in the Abajo Mountains, Manti-Lasal National Forest, Monticello Ranger District*; Forest Health Protection Report OFO-BE-10-03; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2010.

248. Hebertson, E.G. *Evaluation of Bark Beetle Projects on the Heber Ranger District, Uinta-Wasatch-Cache National Forest, Heber Ranger District*; Forest Health Protection Report OFO-TR-11-06; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2011.

249. Hebertson, E.G. *Review of Western Bark Beetle Projects on the Pinedale and Big Piney Ranger Districts, Bridger-Teton National Forest*; Forest Health Protection Report OFO-TR-11-17; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2011.

250. Blackford, D.C. *A Biological Evaluation of Bark Beetles in the Uinta-Wasatch-Cache National Forest, Evanston, Mountain View, Heber, and Kamas Ranger Districts*; Forest Health Protection Report OFO-BE-11-03; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2011.

251. Blackford, D.C. *A Biological Evaluation of Forest Health in the Cold Springs Timber Sale Project Area, Uinta-Wasatch-Cache National Forest, Heber Ranger District*; Forest Health Protection Report OFO-BE-13-02; USDA Forest Service, Intermountain Region: Ogden, UT, USA, 2013.

Appendix

Table A1. A chronology of historic spruce beetle outbreaks in Utah and Wyoming, from 1905–2013 (NF is National Forest; RD is Ranger District).

Year	Outbreak	State	Source
1905	Manti NF	Utah	[103]
1916	Dixie NF; Aquarius Plateau	Utah	[1]
1937	Dixie NF, Cedar City RD	Utah	[213]
1940	Dixie NF, Cedar City RD	Utah	[214]
1944	Dixie NF, Cedar RD; Cedar Breaks	Utah	[215]
1955	Dixie NF; Boulder Top	Utah	[216]
1955	Bridger Teton NF; Gros Ventre, Hoback	Wyoming	[217]
1957	Ashley, Unita, Wasatch NFs; Uinta Mountains	Utah	[216,218]
1961	LaSal NF; Monticello RD; Abajo Peak	Utah	[219]

Table A1. *Cont.*

Year	Outbreak	State	Source
1962	Dixie NF, Teasdale RD; Aquarius Plateau, Griffin Springs	Utah	[219]
1967	Fishlake NF, Loa RD; Hilgard Peak	Utah	[220]
1970	Manti-LaSal NF, Ephraim RD; Huntington Canyon	Utah	[221]
1970	Fishlake NF, Beaver RD	Utah	[222]
1978	Uinta NF, Heber RD; Mill Hollow	Utah	[223]
1978	Bridger-Teton NF, Jackson RD	Wyoming	[224]
1981	Manti LaSal NF, Moab RD	Utah	[225]
1984	Manti-LaSal NF, Moab RD	Utah	[226]
1984	Manti-LaSal NF, Monticello RD	Utah	[226]
1986	Manti-LaSal NF, Sanpete RD; Twelvemile	Utah	[3]
1987	Manti-LaSal NF, Sanpete RD; South Manti	Utah	[227]
1987	Manti LaSal NF, San Pete RD; Geyser Pass	Utah	[228]
1989	Bridger-Teton NF	Wyoming	[224]
1989	Dixie NF, Cedar City RD; Midway Face	Utah	[229]
1989	Wasatch-Cache NF, Evanston RD; Whitney Reservoir	Utah	[230]
1989	Fishlake NF, Loa RD, Neff's Reservoir	Utah	[231]
1990	Manti-LaSal NF, Sanpete RD; Timber Canyon	Utah	[232]
1994	Wasatch-Cache NF, Kamas RD; Humpy Creek	Utah	[233]
1995	Manti-Lasal NF, Moab RD; Lasal Pass	Utah	[234]
1995	Wasatch-Cache NF, Kamas RD; Hoyt peak	Utah	[235]
1995	Dixie NF, Escalante NF, Coyote Gulch	Utah	[236]
1996	Wasatch-Cache NF, Ogden RD; Monte Cristo Ridge	Utah	[237]
1996	Wasatch-Cache NF, Logan RD; Bear Hodges	Utah	[238]
1996	Manti-Lasal NF, Sanpete RD; South Tent	Utah	[239]
1998	Manti-Lasal NF, Monticello RD; Indian Creek	Utah	[240]
1998	Manti-Lasal NF, Monticello RD, North Creek	Utah	[241]
1998	Fishlake NF, Beaver RD; South Fork Beaver River	Utah	[242]
2000	Dixie NF, Escalante RD; Barney Top	Utah	[243]
2002	Fishlake NF, Fremont RD; Fishlake Hightop	Utah	[244]
2004	Manti-LaSal NF, Sanpete RD; Huntington Canyon	Utah	[245]
2004	Uinta NF, Heber RD; Bryant's Fork	Utah	[246]
2008	Manti-LaSal NF, Monticello RD; North Creek	Utah	[247]
2008	Uinta-Wasatch-Cache NF, Heber RD; Wolf Creek	Utah	[248]
2008	Bridger-Teton NF, Pinedale RD; Elkhart	Wyoming	[249]
2010	Uinta-Wasatch-Cache NF, Kamas, Evanston, Mountain View RDs; Whitney Reservoir	Utah	[250]
2012	Uinta-Wasatch-Cache NF, Heber RD; Cold Springs	Utah	[251]