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Article

Douglas-Fir Tussock Moth- and Douglas-Fir Beetle-Caused Mortality in a Ponderosa Pine/Douglas-Fir Forest in the Colorado Front Range, USA

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Abstract: An outbreak of the Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough, occurred in the South Platte River drainage on the Pike-San Isabel National Forest in the Colorado Front Range attacking Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Stocking levels, species composition, and tree size in heavily and lightly defoliated stands were similar. Douglas-fir tussock moth defoliation resulted in significant Douglas-fir mortality in the heavily defoliated stands, leading to a change in dominance to ponderosa pine, *Pinus ponderosa* Lawson. Douglas-fir beetle, *Dendroctonus pseudotsuqae* Hopkins, populations increased following the defoliation event but caused less mortality, and did not differ between heavily and lightly defoliated stands. Douglas-fir tussock moth-related mortality was greatest in trees less than 15 cm dbh (diameter at 1.4 m above the ground) that grew in suppressed and intermediate canopy positions. Douglas-fir beetle-related mortality was greatest in trees larger than 15 cm dbh that grew in the dominant and co-dominant crown positions. Although both insects utilize Douglas-fir as its primary host, stand response to infestation is different. The extensive outbreak of the Douglas-fir tussock moth followed by Douglas-fir beetle activity may be associated with a legacy of increased host type growing in overstocked conditions as a result of fire exclusion.

Keywords: *Orgyia pseudotsugata*; *Dendroctonus pseudotsugae*; douglas-fir tussock moth; douglas-fir beetle; forest insects; defoliators; bark beetles

1. Introduction

The current structure and composition of forested ecosystems is the result of the history of disturbance agents operating in isolation or in concert. Among the disturbance agents shaping forests are biotic agents, such as insects and diseases, and abiotic agents, such as fire and blowdown events [1–3]. An understanding of the combined effects of disturbance agents is crucial for explaining the ecology of these ecosystems, the results and consequences of their effects, and how these processes affect ecosystem services and management planning activities.

The Colorado Front Range extends from the Arkansas River north to the Laramie and Medicine Bow Ranges close to the Colorado-Wyoming border, on the east side of the Continental Divide. Forests in the region exhibit a gradient in vegetation based on elevation and moisture from open ponderosa pine, *Pinus ponderosa* Lawson, forests at lower elevations through montane conifer forests to sub-alpine forests at higher elevations [4]. Ponderosa pine, and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, are found in mixed-species montane forests. Ponderosa pine generally dominates south- and east-facing aspects while Douglas-fir generally dominates north- and west-facing aspects due to increased moisture and cooler temperatures.

Two native insects capable of causing Douglas-fir mortality are always present in these forests: the Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough, and the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. Neither of these insects has historically caused extensive tree mortality in the Colorado Front Range since written records are available, but both may be becoming more common in recent years and occasionally exhibit eruptive populations. The Douglas-fir tussock moth (DFTM) is widely distributed in North America from British Columbia south to California with its eastern edge from Montana south to New Mexico and Arizona [5]. Outbreak populations of the insect have resulted in extensive tree mortality across the West [6–8]. Besides Douglas-fir, primary hosts include white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., and grand fir, *Abies grandis* (Douglas) Lindl., neither of which is native to our study area. The DFTM exhibits one generation per year, overwintering in the egg stage in host tree foliage. Adults are active during summer and into the fall. Females are flightless so primary dispersion is by the first instar larvae which suspend on silken threads from the foliage, facilitating wind transport to other host trees, a behavior called “ballooning”. Outbreaks tend to be brief, most commonly one to three years but can persist as long as seven years. Outbreaks collapse primarily by the pressure exerted by parasites, predators, and entomopathogens. Defoliation by the insect can result in top-kill or tree mortality. Defoliation also results in growth reduction, although in the long-term growth rates may increase in surviving trees as a result of tree mortality of surrounding trees or increased nutrient availability, or both [9,10].

The Douglas-fir beetle (DFB) is the most important tree-killing bark beetle associated with Douglas-fir and occurs from British Columbia and Alberta, through the western US from California east to Colorado and Arizona and south to Chihuahua, Mexico [11]. The insect is usually present in low densities, attacking the underside of downed trees or trees damaged by other agents such as root disease, defoliation, fire injury, wind, and lightning [12–15]. Eruptive populations usually develop after fires, blowdowns, or defoliation events [16,17]. Outbreak populations of DFB cause extensive tree mortality across the central and Northern Rockies and the Pacific Northwest [18–21]. Douglas-fir beetle attacks primarily large diameter trees in highly stocked stands dominated by Douglas-fir, especially trees with reduced growth [16,22]. The insect exhibits a single generation per year and overwinters as an adult or larva. Flight periodicity varies across its range. In the Colorado Front Range peak flight occurs in mid to late June [23].

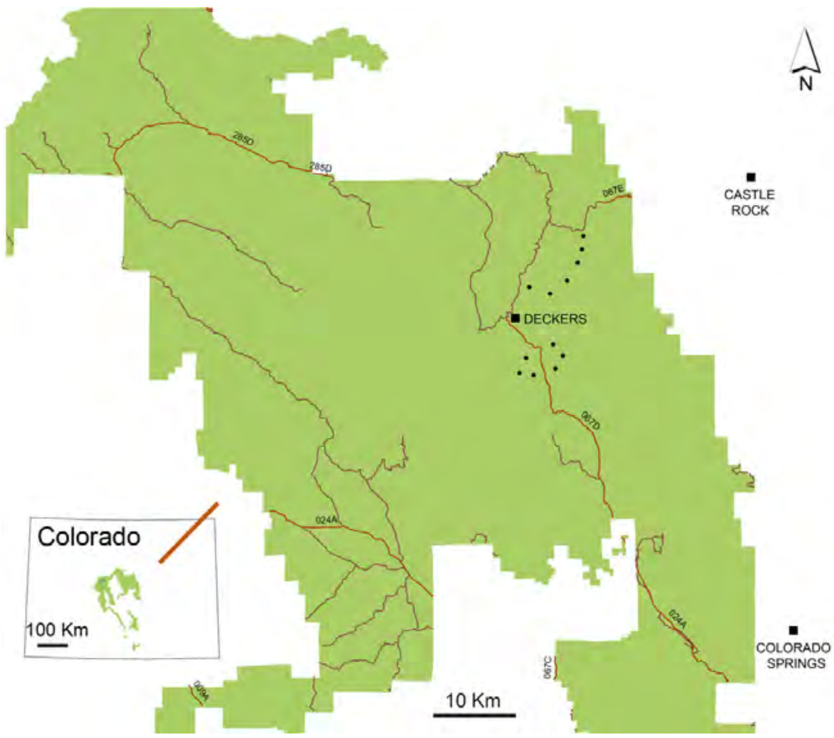
From 1993 through 1995 a DFTM outbreak occurred in parts of the Pike-San Isabel National Forest in central Colorado. Though the moth is native to the area, this was the first recorded large wildland outbreak in the Colorado Front Range [24]. Defoliation was first noted in 1993 on approximately 120 ha along West Creek on the South Platte Ranger District. The outbreak grew to encompass 7300 ha, and collapsed by 1995 [24]. Douglas-fir beetle populations also increased during and following the tussock moth outbreak. Prior to the DFTM outbreak DFB populations were at endemic levels, but by 1995 were attacking trees that had not been defoliated [25]. There are needs for assessing effects of these disturbance agents, determining whether increases in their occurrence result from land management legacies, facilitated by climate change [26], or intrinsic population dynamics of the insect and determining how forest structure and composition are affected. The main goal of this study was to examine how these two insects contribute to changes in forest structure. Research questions posed in this study were to determine: (1) if existing forest conditions were correlated with the level of defoliation caused by DFTM; and (2) if DFTM and DFB changed forest structure equally or differentially based on levels of tree mortality and the tree sizes each killed in heavily and lightly defoliated stands.

2. Experimental Section

2.1. Study Area

The study site was located in the South Platte Ranger District of the Pike-San Isabel National Forest in central Colorado, USA (Figure 1). The area comprised mixed stands of Douglas-fir and ponderosa pine between 2300 and 2400 m elevation, which is where most of the defoliated stands occurred. The approximate geographical centroid for the study site is at UTM 13S 487524, 4349410 (datum NAD27). Thirty-year temperature maximum and minimum normals from 1971 to 2000 are 5.3 °C and −8.8 °C in January, respectively, and 27.1 °C and 10.3 °C, respectively, in July. Precipitation normals for the same period were 17.0 mm and 78.2 mm for January and July, respectively (Prism Climate Group, http://www.prism.oregonstate.edu/, last accessed 6 March 2014). Plant association in the area is described as *Pinus ponderosa-Pseudotsuga menziesii*/*Muhlenbergia montana* [27]. The forest primarily offers recreational activities and watershed protection. Besides Douglas-fir and ponderosa pine, occasional trembling aspen (*Populus tremuloides* Michx), Engelmann spruce (*Picea engelmannii* Parry ex Engelmann), and juniper (*Juniperus* spp.) were present on our study sites.

Figure 1. Study site locations in the South Platte Ranger District, Pike-San Isabel National Forest in central Colorado, USA. Red lines indicate roads, black dots indicate plot locations, and green shading represents National Forest lands.



2.2. Sampling

The defoliated area was delineated using aerial survey data from the US Forest Service, Forest Health, in Lakewood, CO, USA [24]. At a broad or landscape level, such as a watershed, DFTM defoliation is patchy and results in a mosaic of different levels of defoliation across affected forests, though almost the entire area exhibits at least some defoliation. Defoliation estimates from aerial surveys are subjective and classify stands by defoliation severity without specific thresholds. We used the aerial survey maps to randomly select six heavily defoliated and five lightly defoliated stands for our sampling. Ten stands were sampled with a cluster design of 10 to 20 plots, with each plot comprised of two 0.02-ha fixed-radius subplots, following protocols developed by Lynch [28]. Sup-plots were spaced 30 m apart, and plots were established along transects that uniformly covered the stand, with 81 m separation between plots. One stand, which was smaller than 6 ha, was sampled with a simple random sample of 10 plots. A total of 98 plots were established across the heavily defoliated stands and 56 across the five lightly defoliated stands.

Within each plot, the following was recorded for each tree ≥2.54 cm; species, diameter at breast height (dbh, measured at 1.4 m above the forest floor), status, and crown position. Status classifications included live, dead from defoliation (completely defoliated crown and no live phloem), dead from DFB attack (successfully colonized trees with fading crowns and the presence of DFB galleries), dead from both DFTM and DFB, alive with DFTM defoliation (partial defoliation with live phloem), pine, occasional trembling aspen (*Populus tremuloides* Michx), Engelmann spruce (*Picea engelmannii* Parry ex Engelmann), and juniper (*Juniperus* spp.) were present on our study sites.

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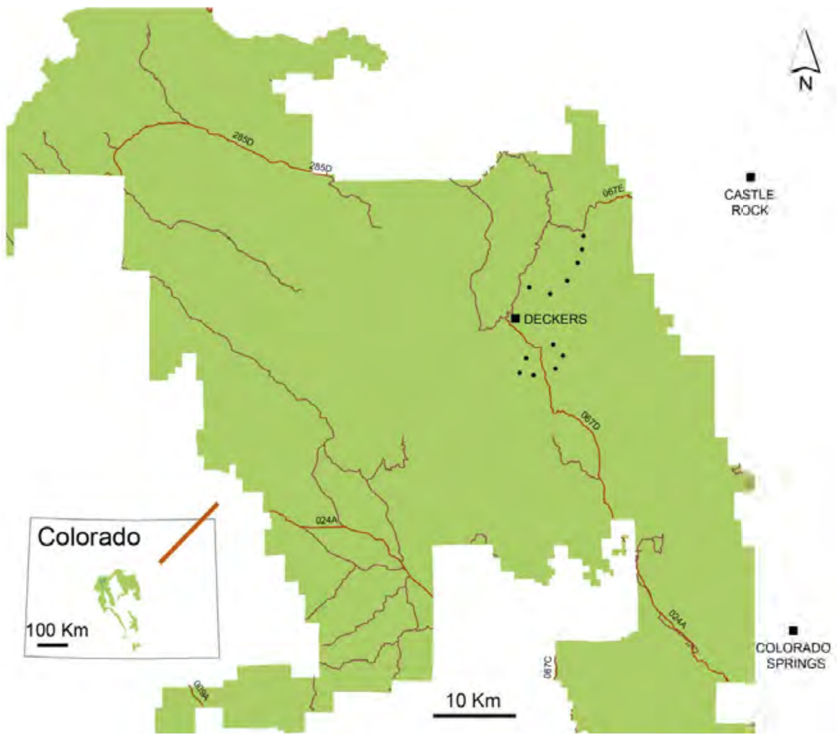

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3. Results

The DFTM outbreak occurred in two general areas, one south of Sprucewood and the other south of West Creek. Douglas-fir beetle populations increased within the defoliated stands attacking defoliated trees [24] and eventually moved into non-defoliated stands surrounding the initial DFTM outbreak (Figure 2). Before the DFTM outbreak, stands that were subsequently heavily or lightly defoliated had similar stocking levels and average dbh of all species combined as well as for Douglas-fir and ponderosa pine individually (Table 1). Douglas-fir tussock moth-related mortality, quantified as stand density, basal area, and percent mortality, was greater in heavily defoliated stands compared to lightly defoliated stands.

The insect outbreaks altered species dominance in the heavily defoliated (Table 1). Post-outbreak, the percent of Douglas-fir stocking was reduced in heavily defoliated stands. Furthermore, the ponderosa pine percent stocking increased significantly in the heavily defoliated stands. There was no difference in percent mortality caused by the DFB between heavily and lightly defoliated stands (Table 1).

Douglas-fir tussock moth and DFB impacted trees of different size classes and canopy positions. Douglas-fir tussock moth-related mortality was significantly associated with smaller diameter classes while DFB-related mortality was associated with larger diameter classes (Chi-square = 607.4, $df = 4$, $p < 0.0001$) (Figure 3). Douglas-fir tussock moth-related mortality was significantly associated with intermediate and suppressed crown positions while DFB-related mortality was associated with dominant and co-dominant crown positions (Chi-square = 212.8, $df = 2$, $p < 0.0001$) (Figure 4). In heavily defoliated stands, across all plots, DFTM-killed trees were significantly smaller (mean dbh 12.2 ± 0.2 cm, $n = 1443$) than DFB-killed trees (mean dbh 33.8 ± 1.0 cm, $n = 94$) in the heavily defoliated stands ($p < 0.001$). Similarly, DFTM-killed trees (mean dbh 12.9 ± 0.9 cm, $n = 73$) were significantly smaller than DFB-killed trees (mean dbh 32.6 ± 1.6 cm, $n = 36$) ($p < 0.001$) in lightly defoliated stands.

Figure 2. Areas affected by Douglas-fir tussock moth in 1994 and 1995, and by Douglas-fir beetle in 1997–2000, as determined by aerial sketch mapping on the Pike-San Isabel National Forest. Data for Douglas-fir beetle was not available prior to 1997.

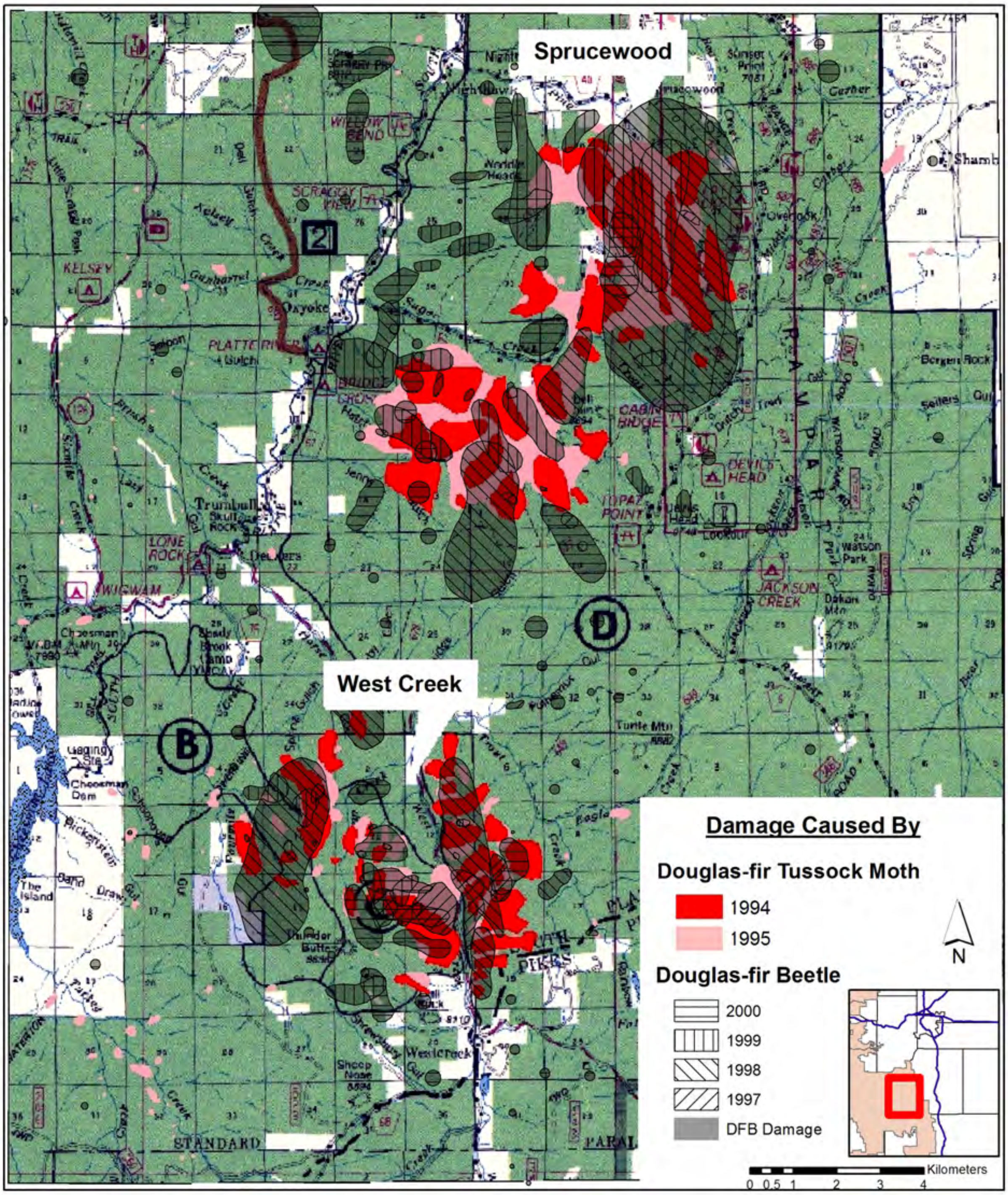


Table 1. Means (±SEM) of density (tph, trees per ha), basal area (m^2/ha), and diameter at breast height (dbh) of all species combined, Douglas-fir, ponderosa pine, Douglas-fir tussock moth- and Douglas-fir beetle-related mortality (DFTM and DFB, respectively) of heavily and lightly defoliated stands in the study area. Asterisks (*) indicate values that are significantly different ($p < 0.05$) for the same variable between heavily and lightly infested stands in the same line (PROC GLIMMIX, SAS), and daggers (†) indicate values of initial condition and post-outbreak that are significantly different ($p < 0.05$) for the same variable in adjacent columns, MRPP test. Pike-San Isabel National Forest, Colorado, USA, 1996–1997.

	Heavily Defoliated Stands (*n* = 6)				**Lightly Defoliated Stands (*n* = 5)**			
	Initial Condition	**Post-Outbreak**	**DFTM-Killed**	**DFB-Killed**	**Initial Condition**	**Post-Outbreak**	**DFTM-Killed**	**DFB-Killed**
Stand Characteristics								
All Species								
Basal Area (m^2/ha)	25.1 (1.8)	8.0 (1.2) *	--	--	22.4 (0.8)	18.6 (2.0) *	--	--
Density (tph)	1115 (101)	307 (31) *	--	--	942 (102)	845 (124) *	--	--
Douglas-fir								
Basal Area (m^2/ha)	19.4 (1.5)	2.4 (0.4) *	12.8 (2.1) *	4.1 (1.7)	15.0 (2.2)	10.6 (3.6) *	1.2 (0.6) *	2.7 (1.4)
Density (tph)	941 (104)	67 (25)	763 (113) *	43.3 (17.5)	657 (137)	309 (186)	68.0 (40) *	30.0 (14.0)
% Basal Area	74.8 (5.4) †	17.5 (5.0) †	--	--	63.9 (10.7)	33.8 (16.2)	--	--
% Density	78.4(3.6) †	18.3 (4.2) †	--	--	65.0 (1.9)	36.1 (15.5)	--	--
Mean dbh (cm)	16.3 (1.6)	14.0 (2.5)	14.0 (1.0)	34.9 (3.4)	16.4 (1.4)	12.6 (1.3)	14.0 (2.0)	35.6 (3.0)
Ponderosa pine								
Basal Area (m^2/ha)	5.6 (1.5)	5.6 (1.4)	--	--	7.1 (2.3)	7.1 (2.3)	--	--
Density (tph)	162 (31)	160 (31)	--	--	246 (94)	246 (94)	--	--
% Basal Area	24.8 (5.5) †	63.0 (7.3) †	--	--	32.9 (10.8)	60.7 (15.0)	--	--
% Density	20.4 (3.5) †	60.6 (6.7) †	--	--	31.1 (10.5)	57.5 (15.0)	--	--
Mean dbh (cm)	19.6 (1.0)	18.9 (1.4)	--	--	18.1 (1.8)	18.1 (1.8)	--	--
Outbreak Effects Percent Douglas-fir mortality								
By basal area			64.5 (8.4) *	17.9 (7.9)			14.0 (8.5) *	14.4 (6.5)
By density			70.9 (15.4) *	7.9 (4.6)			15.4 (9.1) *	6.2 (3.3)

Figure 3. Total number (therefore no standard error) of live, Douglas-fir tussock moth-killed, and Douglas-fir beetle-killed trees across all plots and across diameter at breast height (dbh) classes. No Douglas-fir beetle-killed trees in the smallest diameter class. Pike-San Isabel National Forest, Colorado, USA, 1996–1997.

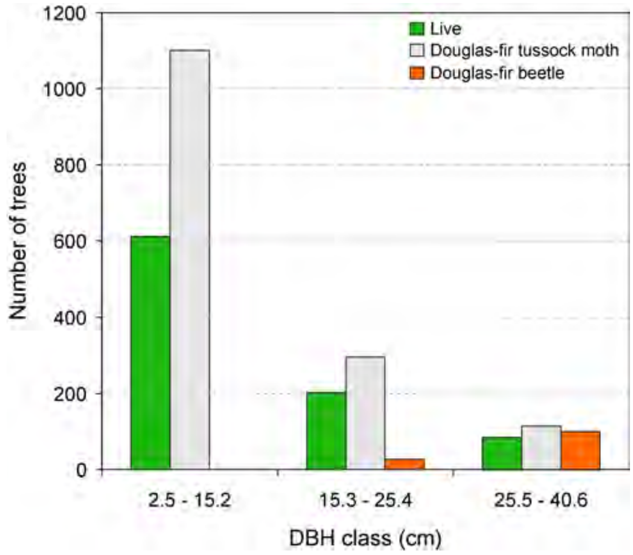
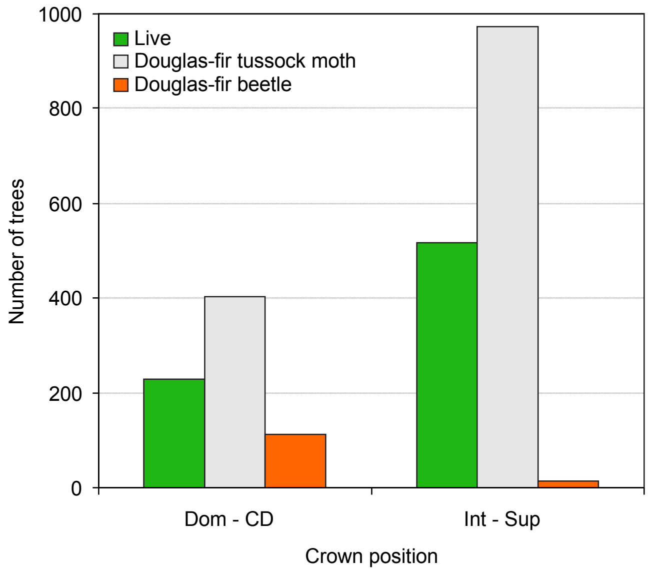


Figure 4. Total number (therefore no standard error) of live, Douglas-fir tussock moth-killed, and Douglas-fir beetle-killed trees across all plots and crown position classes; dominant and co-dominant (Dom-CD) and intermediate and suppressed (Int-Sup). Pike-San Isabel National Forest, City, Colorado, USA, 1996–1997.



4. Discussion

This study examined possible stand conditions correlated with the DFTM outbreak and forest vegetation response to the outbreak. We did not detect pre-outbreak differences in stand conditions between heavily and lightly defoliated stands, yet mortality caused by defoliation in the heavily defoliated stands reduced Douglas-fir representation particularly in smaller trees growing in the suppressed and intermediate crown classes. As a result we observed an increase in the proportion of ponderosa pine in these stands. Species composition and tree density and basal area levels in our study sites were similar to those found in ponderosa pine/Douglas-fir forests in other Colorado Front Range studies, particularly in north-facing aspects [22,31].

Species composition and stand structure of our heavily defoliated sites were not significantly different than in lightly defoliated sites, though other studies found that species composition and stand structure do contribute to DFTM susceptibility [32,33]. Site and stand conditions within DFTM infestations exhibit variation across the geographic extent of the insect, and our study sites are less variable in structure and species composition than either the northern Idaho [32] or southern California [33] situations, reflecting general forest conditions in our area. The three studies also differ substantially in the lower size limit of trees included in the descriptive statistics, so basal area and density reported in the studies are not directly comparable. Grand fir-dominated stands that are overmature, dense, and multistoried are more susceptible. Stoszek *et al.* [32] developed models for mixed grand fir and Douglas-fir stands in northern Idaho, and found that the best predictors of DFTM defoliation included slope position, stand age, host occupancy (ratio of total stand density with respect to site index), and proportion of stocking in host species. In general, stands at lower elevations and those on ridge tops or positioned high in the slope are more likely to be infested. In southern California, stands located in areas not previously known to experience DFTM outbreaks, Coleman *et al.* [33] also found that DFTM occurred in stands with a greater proportion of density and stocking in host species compared to non-defoliated stands. The proportion of density and basal area represented by host trees was somewhat higher in our stands (78% and 74%, respectively) than that observed by Coleman *et al.* [33] in southern California (70% and 64%, respectively), but this probably reflects the smaller diameter limit used in our study. Our study focused on stand conditions; examination of a more extensive affected area would be needed to assess site factors such as elevation or position on the slope and their influence on susceptibility to DFTM.

Wickman [7,8] examined white fir mortality from DFTM defoliation in the Warner and Sierra Nevada Mountains in northern California, and found that defoliation-related mortality was greatest in trees 2.5 to 15 cm dbh. This is consistent with our findings of greater damage to suppressed and intermediate trees in the smaller diameter class. Douglas-fir beetle populations increased in the study sites during the DFTM outbreak and continued to expand after the DFTM outbreak collapsed [24]. Bark beetle population increases after DFTM defoliation has been observed elsewhere. Wright *et al.* [12] reported increased number of attacks by the fir engraver, *Scolytus ventralis* LeConte, and DFB one and two years after defoliation and suggested that reduced host resistance may facilitate bark beetle attacks. Wickman [7,8] also reported fir engraver attacks in trees defoliated by the DFTM. Douglas-fir beetle outbreaks have also been documented following western spruce budworm (WSB), *Choristoneura occidentalis* Free., defoliation. Lessard and Schmid [17] reported increased DFB emergence from WSB-defoliated trees in the Colorado Front Range. Hadley and Veblen [34] and Hadley [35] also reported DFB populations from areas defoliated by WSB populations in the Colorado Front Range. By the time our sites were sampled, DFB caused mortality in both heavily and lightly defoliated stands. This mortality was concentrated in the larger diameter classes, portraying the preference of the insect for larger diameter trees [16,20,22].

Douglas-fir tussock moth populations have a propensity to concentrate around initial infestation sites [36,37], so the distribution of DFTM-related tree mortality is probably associated with spatial location of early infestation foci. Douglas-fir tussock moth dispersal primarily through "ballooning" of larvae to nearby trees. Douglas-fir tussock moth does not typically disperse large distances, usually remaining within 200 m of an infested tree [38].

Distribution of DFB-related tree mortality is influenced by the distribution of basal area across the stand, as the beetle prefers large trees in heavily stocked areas [39]. Douglas-fir beetle has greater dispersal ability than does DFTM, and is capable of initiating new infestations 2.5 km away from previous year's infestations [40]. This means that in general DFTM infestations are somewhat localized, resulting in a mosaic of small patches comprised of primarily larger-diameter trees and dominated by ponderosa pine, depending on the potential increase of DFB populations. These conditions result in reduced susceptibility to DFTM until surviving and recruiting understory trees grow to susceptible stages. However, depending on the density of surviving large Douglas-fir trees, stands may be susceptible to future DFB outbreaks [16,20,22]. The dispersal ability of the DFB results in larger landscapes being affected, resulting in vegetation mosaics composed of smaller trees reducing susceptibility to DFB outbreaks but maintaining stand conditions susceptible to DFTM.

In the Colorado Front Range, DFTM has historically been more frequent in urban environments than in wildland forests [24]. Three previous, much smaller, defoliation events are documented [24]. In 1937, about 80 hectares were defoliated about 60 km southeast of our study site, just outside of Colorado Springs, CO, USA. In the late 1940's, a small infestation was reported in Evergreen, Colorado, about 40 km north of our study area. Extent is unknown, but insecticide treatments were applied and DFB populations increased after the defoliation event. In early 1980s, an infestation occurred about 10 km west of our study sites: it is presumed to have been small because extent was not reported, and an extensive outbreak of any forest defoliator would have been well documented during that time period. More recently, from 2004 through 2007 and at the time of this writing another outbreak is occurring along the Rampart Range, located about 5 km east of our study site. On the other hand, though DFB outbreaks in the Colorado Front Range are not frequent, they occur more often than do DFTM outbreaks, and they are more extensive. DFB outbreaks often develop following WSB defoliation. Prior to the one studied here, outbreaks have been reported in 1934–1938, 1950–1951, and 1984–1990 [41].

The combined effects of DFTM and DFB shifted stand structure to a more narrow tree size distribution of Douglas-fir by removing the smaller (DFTM-killed) and larger (DFB-killed) trees. This has also been observed when DFB outbreaks follow WSBW outbreaks [34,35]. Western spruce budworm is a more frequent and severe defoliator of Douglas-fir in the Colorado Front Range [42] than DFTM, and outbreaks are sometimes followed by DFB population increases [17,34,35]. Hadley and Veblen [34] reported that WSB outbreaks caused high mortality of small-diameter and suppressed seedling-sized, Douglas-fir, while DFB killed larger diameter trees. Although extensive overstory Douglas-fir mortality resulted from a WSB outbreak along the Colorado Front Range in the mid-1970s to 1980s, mortality was greater in understory trees [34,35]. Hadley [35] suggested that the combined activity of WSB and DFB can shift species dominance to non-host species, create a narrower tree size distribution by removing the larger and smaller trees, and reduces the vertical diversity of the affected stands, similar to what we observed here at a smaller scale. Scale differences could be a result of the limited dispersal ability of DFTM [38] and the shorter duration of DFTM outbreaks compared to WSB [43].

In central Colorado, forest disturbances including fire at various scales and other disturbance agents such as insect and diseases, patterns of seedling establishment, and other factors resulted in a heterogeneous forest condition across the landscape [31]. In the Southwestern USA, in ponderosa pine forests, changes in fire frequency resulted in a significant increase in stem densities and a shift in species composition toward more shade tolerant, fire-sensitive species [44–46]. Though fire regimes in Colorado Front Range ponderosa pine forests are similar, high-severity landscape-scale fire plays a larger role than in the Southwest [47,48]. Studies at nearby Cheeseman Reservoir show that stands, once dominated by open-grown, low-density, ponderosa pine are now high-density stands dominated by Douglas-fir as a result of fire exclusion in the 20th Century [31]. These high-density stands can exhibit increased susceptibility to insects by increasing stand stress due to overstocking or an abundance of host, or both [20,22]. Fire is the most important abiotic disturbance agent driving forest vegetation structure and spatial patterning in the Colorado Front Range [31,47–49]. Fire regimes in the Colorado Front Range are very complex and are influenced by elevation, climate, and past land use practices among others. Veblen [49] indicated that in the northern Front Range high density stands can result from high intensity fires at higher elevations (>2400 m) and fire exclusion in lower elevations.

Western spruce budworm outbreaks in the Southern Rockies became more severe and synchronous beginning about 1950 [42,50]. Across the 19th and 20th centuries Southwestern and southern Rocky Mountain forests were impacted by fire exclusion [51–53]. This increase in synchronicity may also be a function of selective logging and increased tree recruitment in the early 1900's due to increased moisture, and intensive and selective logging at approximately the same time (see [42]). These factors produced an abundance of stands dominated by shade-tolerant species growing in high density conditions with closed multi-storied canopies which can favor forest insect outbreak dynamics, especially for defoliators on shade-tolerant fire-intolerant species such as DFTM and WSB [42,50,54].

The recent DFTM outbreak in southern California, the first recorded in the area occurred in stands where stand species composition had shifted from pine-dominated stands to a pine-fir mixed stand perhaps due in part to a change in fire regime. Land use changes and reduced thinning may have also have contributed to the change [33]. As it relates to the DFTM in the Colorado Front Range, a similar interpretation of species composition changes favoring DFTM is certainly plausible and needs to be studied, as disturbance patterns are expected to become more frequent and intense under a climate change scenario. Stand response of these altered forests to defoliation by DFTM and followed by DFB is similar to stand response observed as a result of WSB outbreaks followed by DFB populations.

5. Conclusions

Douglas-fir tussock moth defoliation was not associated with current stand stocking, species composition, or tree size at the stand level in the study area. However, across all stands DFTM killed mostly smaller diameter trees in suppressed and intermediate crown positions, while DFB killed larger trees in the dominant and co-dominant diameter classes. Heavily defoliated stands exhibited a shift in dominance from Douglas-fir to ponderosa pine and a shift toward a more narrow size distribution of

Douglas-fir. Mixed conifer montane forests in the Colorado Front Range may respond to DFTM and DFB similarly to their response to the combined effects of WSB and DFB outbreaks.

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Author Contributions

José Negrón, Ann Lynch, and Willis Schaupp identified the need for the work, developed field protocols, and led field plot establishment. José Negrón led the data analysis and wrote the first draft of the paper. Javier Mercado assisted with data processing, analysis, and preparing figures. All authors contributed to writing and editing.

Conflicts of Interest

The authors declare no conflict of interest.

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Figure 3. Total number (therefore no standard error) of live, Douglas-fir tussock moth-killed, and Douglas-fir beetle-killed trees across all plots and across diameter at breast height (dbh) classes. No Douglas-fir beetle-killed trees in the smallest diameter class. Pike-San Isabel National Forest, Colorado, USA, 1996–1997.

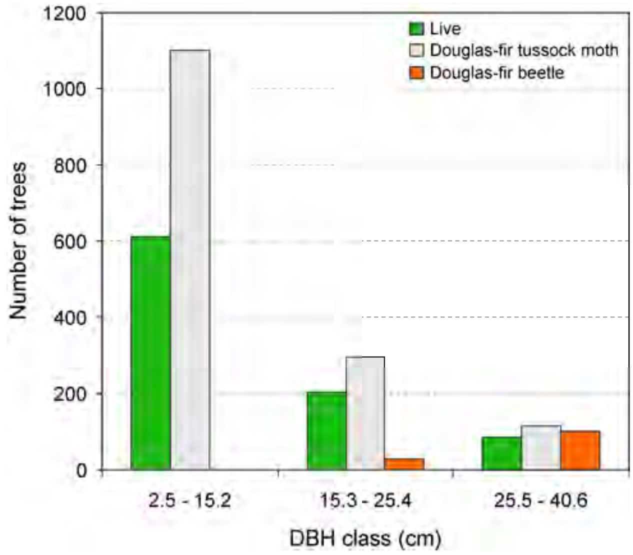
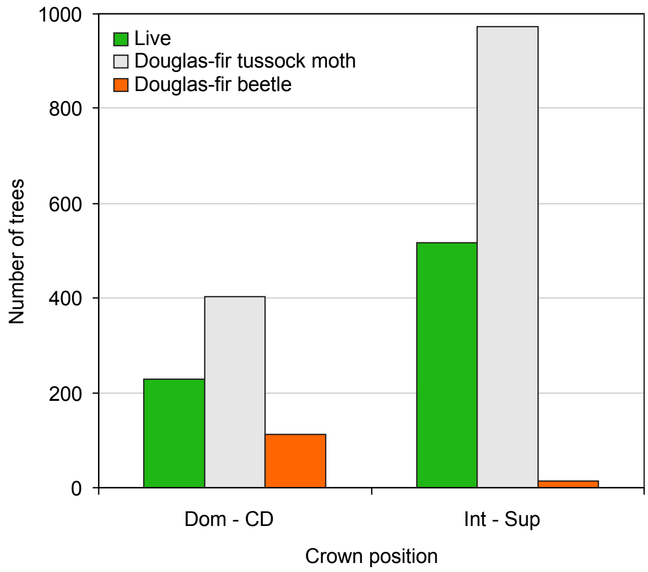


Figure 4. Total number (therefore no standard error) of live, Douglas-fir tussock moth-killed, and Douglas-fir beetle-killed trees across all plots and crown position classes; dominant and co-dominant (Dom-CD) and intermediate and suppressed (Int-Sup). Pike-San Isabel National Forest, City, Colorado, USA, 1996–1997.



4. Discussion

This study examined possible stand conditions correlated with the DFTM outbreak and forest vegetation response to the outbreak. We did not detect pre-outbreak differences in stand conditions between heavily and lightly defoliated stands, yet mortality caused by defoliation in the heavily defoliated stands reduced Douglas-fir representation particularly in smaller trees growing in the