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Outbreaks of Douglas-Fir Beetle Follow Western Spruce Budworm Defoliation in the Southern Rocky Mountains, USA

Hailey M. Cole [1], Robert A. Andrus [2], Cori Butkiewicz [1], Kyle C. Rodman [3], Olivia Santiago [4], Niko J. Tutland [4], Angela Waupochick [1] and Sarah J. Hart [4,*]

[1] Department of Forest and Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706, USA; hmcole@wisc.edu (H.M.C.); cori.butkiewicz@gmail.com (C.B.); waupochick@wisc.edu (A.W.)
[2] School of the Environment, Washington State University, Pullman, WA 99164, USA; robert.andrus@wsu.edu
[3] Ecological Restoration Institute, Northern Arizona University, Flagstaff, AZ 86011, USA; kyle.rodman@nau.edu
[4] Department of Forest and Rangeland Stewardship, Colorado State University, 1472 Campus Delivery, Fort Collins, CO 80523, USA; o.santiago@colostate.edu (O.S.); niko.tutland@colostate.edu (N.J.T.)
* Correspondence: sarah.hart@colostate.edu; Tel.: +1-970-491-6921

Abstract: Changes in climate are altering disturbance regimes in forests of western North America, leading to increases in the potential for disturbance events to overlap in time and space. Though interactions between abiotic and biotic disturbance (e.g., the effect of bark beetle outbreak on subsequent wildfire) have been widely studied, interactions between multiple biotic disturbances are poorly understood. Defoliating insects, such as the western spruce budworm (WSB; *Choristoneura freemanni*), have been widely suggested to predispose trees to secondary colonization by bark beetles, such as the Douglas-fir beetle (DFB; *Dendroctonus pseudotsugae*). However, there is little quantitative research that supports this observation. Here, we asked: Does previous WSB damage increase the likelihood of subsequent DFB outbreak in Douglas-fir (*Pseudotsuga menziesii*) forests of the Southern Rocky Mountains, USA? To quantify areas affected by WSB and then DFB, we analyzed Aerial Detection Survey data from 1999–2019. We found that a DFB presence followed WSB defoliation more often than expected under a null model (i.e., random distribution). With climate change expected to intensify some biotic disturbances, an understanding of the interactions between insect outbreaks is important for forest management planning, as well as for improving our understanding of forest change.

Keywords: disturbance interactions; biotic disturbances; *Pseudotsuga menziesii*; *Dendroctonus pseudotsugae*; *Choristoneura freemani*; bark beetles

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1. Introduction

Over the past two decades, forests across the western United States have experienced widespread reductions in growth and increases in tree mortality due to outbreaks of native insects [1]. This has created cascading consequences for key ecosystem services, including timber supply [2], recreation [3], wildlife habitat [4], and carbon sequestration [5]. These recent outbreaks have been facilitated by warm and dry conditions, which accelerate insect reproduction and development rates [6–9], expand the suitable habitat for insects to higher latitudes and elevations [10], and weaken host tree defense mechanisms [11–13]. Due to the fact that warming is forecasted to increase throughout the 21st century [14], future climate conditions are expected to facilitate more extensive and frequent outbreaks [15,16]. Critically, such alterations to disturbance regimes are expected to increase rates of disturbance interactions [17]. However, there is considerable uncertainty about the consequences of increased rates of disturbance interactions [18,19], particularly when considering interactions between irruptive insects.

Disturbances may interact when they overlap in space within a relatively short period [17,19]. Linked disturbances occur when one disturbance affects the occurrence, timing, or severity of a subsequent disturbance [20]. For example, stand-replacing wildfires may decrease the probability of subsequent bark beetle outbreaks until enough time has passed to allow trees to grow into sizes that can support beetle populations [21]. Overlapping disturbances may also result in compound effects, when one disturbance alters the capacity for the ecosystem to recover from the following disturbance [22]. For instance, severe outbreaks of spruce beetle (*Dendroctonus rufipennis*), followed by wildfire, may lead to low post-fire regeneration of spruce, altering species composition and in some cases, extending the pre-forest stage of stand development [23]. Understanding when and where disturbance interactions are likely to occur is critical for forecasting ecosystem change and for developing effective adaptive management strategies [24].

Bark beetles (Curculionidae: Scolytinae) and defoliating budworms (*Choristoneura* spp.) are among the few native insects capable of causing widespread reductions in tree growth and/or mortality in a single year. Indeed, in the western United States, bark beetles and budworms have recently affected forests across ca. 22.3 and 9.5 million ha, respectively (1990–2020) [25]. Nearly half (47%) of the area affected by recent bark beetle outbreaks has been attributed to the mountain pine beetle (*Dendroctonus ponderosae*), which predominantly feeds upon pines (*Pinus* spp.). Nonetheless, outbreaks of the Douglas-fir beetle (DFB; *Dendroctonus pseudotsugae*) have affected two million ha of Douglas-fir (*Pseudotsuga menziesii*) forest in recent decades. Notably, Douglas-fir forests have also experienced extensive defoliation due to the western spruce budworm (WSB; *Choristoneura freemani*), which has caused most (83%) of the recent tree defoliation in the West (1990–2020) [25]. Douglas-fir dominated forests are widespread, economically important, and evidently susceptible to outbreaks of both irruptive phloem feeders (i.e., DFB) and folivores (i.e., WSB), highlighting the need to understand potential interactions between irruptive insects.

Defoliators, such as the WSB, are specialist herbivores that preferentially feed upon young buds and new foliage of their host tree species [26]. Defoliation can occur throughout the tree but is most prominent in upper crowns and outer branch tips. WSBs can cause bare tops, bare branch tips, or thin crowns on host trees. Typically, WSBs exist at endemic or low population levels, which cause only minimal defoliation. During outbreaks, populations increase by several magnitudes, causing severe defoliation, reductions in tree growth, and occasional tree mortality [27]. Outbreaks occur when several ecological thresholds are crossed and negative feedbacks among the WSBs, host trees, and natural enemies no longer constrain WSB populations. Female WSB deposit eggs on both original host trees and new trees, spreading the outbreak. WSB development on a single tree varies, but complete defoliation typically takes 4–5 years. Stand-scale infestations typically persist for approximately a decade [28] and eventually collapse due to declines in resource availability and increases in natural enemies [26]. Refoliation may occur months to years following defoliation; however, the recovery of radial growth to pre-outbreak conditions typically takes several years [27,28].

The DFB is an irruptive phloem feeder that colonizes Douglas-fir trees by boring through the bark, where they mate and oviposit. Bark beetles' colonization of a tree's phloem tissues, along with the introduction of pathogenic fungi they carry, typically stops the movement of water and nutrients, and ultimately results in tree death [29]. While DFB typically exist at low population levels and attack weakened trees, populations may irrupt in response to factors that accelerate beetle population dynamics (e.g., temperature) or decrease host resistance to infestation (e.g., drought stress). As populations increase, coordinated mass attacks allow bark beetles to overcome the primary defense mechanisms of their host trees, notably resin flow, which can physically expel or encase attacking beetles, and chemical defense compounds, such as monoterpenes [30]. Decreases in carbon uptake caused by defoliation are hypothesized to increase the susceptibility to subsequent bark beetle attacks by decreasing the ability of trees to produce defensive structures (i.e., resin

ducts) and compounds [31,32]. However, this apparent disturbance linkage has received relatively little study, particularly across broad landscapes.

In this study, we analyze interactions between outbreaks of WSB and DFB in Douglas-fir dominated forests of the Southern Rocky Mountains, which have experienced outbreaks of WSB and DFB over broad areas within the past 20 years. Specifically, we asked: Does defoliation by WSB increase the probability of subsequent DFB outbreaks? We expect that trees defoliated by WSB are more susceptible to subsequent infestation by DFB, and thus stands defoliated by WSB will experience higher rates of DFB outbreaks than stands unaffected by WSB.

2. Materials and Methods

2.1. Study Area

The study area is the Southern Rocky Mountain ecoregion (SRME) [33], which covers ca. 145,000 km^2 in Colorado, southern Wyoming, and northern New Mexico, USA (Figure 1). Ranging from 35.5–42.8° N and 103.8–109.0° W, the SRME is characterized by complex topography (elevations c. 1500 to 4400 m) and a continental climate with warm summers (mean [range] July maximum temperature 24.1 °C [12.5 to 32.9]), cold winters (January minimum temperature −12.3 °C [−21.3 to −5.4]), and diurnal fluctuations of 10 °C or more. Precipitation is bimodal (annual precipitation 625 mm [214 to 1875]), with peaks in March-May and July-August; the importance of summer precipitation increases to the south and east [34].

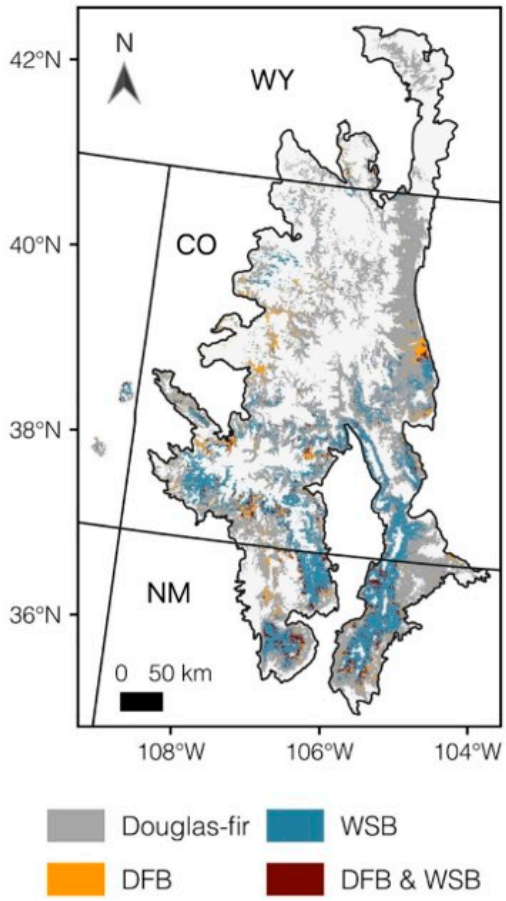

Figure 1. The Southern Rocky Mountain ecoregion (i.e., EPA Level III Ecoregion #21) and the range of Douglas-fir (gray), recent defoliation due to western spruce budworm (blue), recent tree mortality due to Douglas-fir beetle (yellow), and their intersection (dark red). Here, presence represents all 960 × 960 m pixels where at least 25% (four or more 240 × 240 m subpixels) listed presence. All layers were restricted to the distribution of Douglas-fir. Lines illustrate state boundaries.

Forests cover approximately 55% of the SRME [35] and tree species composition and disturbance regimes vary drastically across latitudinal and elevational gradients [36]. Douglas-fir is an important tree species at intermediate forested elevations in the SRME (c. 1900–3000 m), where it occupies approximately 30,000 km^2 in the region [37]. In the SRME, Douglas-fir commonly co-occurs with ponderosa pine (*Pinus ponderosa*) on warm/dry sites and white fir (*Abies concolor*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*) on cool/wet sites. In addition to WSB and DFB, other biotic agents also affect Douglas-fir, including Douglas-fir tussock moth (*Orygia pseudotsugae*), dwarf mistletoe (*Arceuthobium douglasii*), pole beetle (*Pseudohylesinus nebulosus*), engraver beetle (*Scolytus unispinosis*), and a range of fungal pathogens (e.g., *Phaeolus* spp., *Armillaria* spp.) [38]. However, WSB and DFB are the most prevalent insect species that affect Douglas-fir. Douglas-fir forests also experienced a wide array of historical (i.e., pre-1900s) fire regimes throughout the SRME, with mean fire return intervals ranging from 10–100+ years [39,40].

2.2. Data

To define the extent of Douglas-fir in the SRME, we used gridded data describing species basal area ca. 2002 (240 × 240 m spatial resolution) from USFS Individual Tree Species Parameter (ITSP) maps [37]. To characterize areas affected by DFB and WSB, we obtained spatial data from USFS Aerial Detection Survey (ADS) program [25] (Table 1), in which, disturbance location, agent, and host are mapped annually by trained observers via airborne sketch mapping. These observers identify damaged trees and note the presence of disturbance agents, such as defoliators and bark beetles. Surveys are conducted in the summer when current year defoliation injury and tree mortality can be distinguished from prior damage. ADS data are useful for characterizing broad-scale trends of forest disturbance. These data represent the most spatially extensive and long-term (i.e., >20 years) remote sensing dataset characterizing forest disturbance due to specific insects [41]. Since outbreaks of DFB and WSB have occurred several times over the last 20 years, we included the entire period of 1999–2019 in our analyses. From ADS data, we only selected polygons where the primary damage-causing agent was listed as western spruce budworm or Douglas-fir beetle. While ADS data often include a description of the primary host species or group of host species, these data have been recorded inconsistently across years and USFS regions (Appendix A, Figure A2). Thus, we included all polygons identified as WSB or DFB, regardless of the host species. To ensure that our results were not sensitive to host species, we repeated all analyses with the subset of ADS polygons where Douglas-fir was listed as the host species (Appendix A, Figure A3). Additionally, given defoliation by WSB may have a greater impact on tree susceptibility to DFB infestation when stand-level defoliation is high and bark beetle populations are low [30], we performed additional sensitivity analyses using the subset of data where damage severity was recorded (Appendix A, Figures A4 and A5).

Table 1. Geospatial data layers.

Variable	Description	Type	Year	Resolution
Aerial detection survey damage areas [25]	Areas of damage and associated attributes, including the primary pest or pathogen causing damage, and severity of injury	Polygon	1999–2019	Compiled at 1:100,000 scale
Burned area boundaries [42]	Historic fire perimeters	Polygon	1984–2018	Compiled at 1:24,000–1:5000 scale
Timber harvest [43]	Management activities that removed forest biomass, reported through Forest Service Activity Tracking System (FACTS) database	Polygon	1850–2019	Digitized using either aerial imagery or GPS field collected points
Aerial detection survey area surveyed [25]	Extent of surveyed areas	Polygon	1999–2019	Compiled at 1:100,000 scale
Fractional cover of individual tree species [37]	The number of 30 × 30 m subpixels predicted to contain the tree species	Raster	ca. 2002	240 × 240 m

2.3. Data Processing

We converted polygon data of WSB and DFB outbreaks to a 240 × 240 m raster grid, aligned with the ITSP map, that listed the presence/absence of each agent for each year. Specifically, we listed agent presence when polygons overlapped with the center of each pixel using the R package 'fasterize' [44]. Because ADS data are most effective at depicting coarse-scale outbreak dynamics (>500 m) [41,45], we aggregated the 240 × 240 m rasters to a 960 × 960 m grid by calculating the proportion of 240 × 240 m pixels affected by WSB or DFB outbreaks within the 960 m pixel. We then listed the presence of outbreak within a 960 m pixel where at least 25% of the underlying 240 m pixels were affected. Similarly, we aggregated rasters of Douglas-fir fractional cover to 960 × 960 m and limited our analyses to only pixels where Douglas-fir occupied at least 25% of the area of each pixel. To test if our results were sensitive to this threshold, we repeated overlay analyses using five other thresholds (6, 12, 38, 50, and 75%), which showed only slight differences (Appendix A, Figure A1).

To reduce the potential effects of other disturbances, we removed the following disturbed areas from our analysis: (1) recent (1984–2018) wildfires [42], (2) management activities that removed forest biomass (e.g., timber harvests) [43], and (3) recent (1999–2019) disturbances by biotic agents other than WSB or DFB [25] (Table 1). Since ADS data are a targeted sampling effort that does not always survey the entirety of a region, we constrained the study area to only areas flown in ADS surveys. We also only included USFS land, where records of past disturbance are most complete, particularly for past management activities.

2.4. Analyses

To test whether prior WSB increases the probability of subsequent DFB outbreak, we used spatial overlay analysis [46], an approach widely used to assess linked disturbances [47,48]. This method compares the observed intersection of two spatial datasets with the expected area of intersection under a random spatial distribution. Here, the independent variable is the presence/absence of WSB, and the dependent variable is the presence/absence of DFB occurring at each time interval after WSB outbreak. A positive departure of the observed area from the expected area indicates a positive relationship between the predictor and response at a given time lag. Because our spatial overlays assessed the entire population and not just samples, all deviations between observed and expected areas are viewed as meaningful ecological differences.

We performed separate spatial overlays for each year in the period 1999–2019, where we overlaid rasters of DFB presence for the focal year with rasters of WSB presence for the preceding 1–10 years. Because co-occurrence of biotic agents may result from similar drivers rather than a causal effect [19], we also quantified the area of DFB that occurred in areas with WSB in the same year or any year in the subsequent ten year-period. For example, for a pixel affected by DFB in 2005, we checked for WSB presence in that pixel from 2005–2015. Finally, we summarized the effect of WSB on DFB by summing the observed and expected areas across all years by temporal lag and threshold used to determine presence. Since ADS data best characterize trends at coarse spatial and temporal scales and that numerous other factors may drive DFB outbreak dynamics, we focus on consistent patterns rather than attempting to identify a specific lag at which WSB outbreak influences subsequent DFB outbreak.

3. Results

DFB and WSB outbreaks were most heavily concentrated in southern latitudes across the study area (Figure 1). Both insects were active throughout the study area during the study period, with the peak activity of WSB and DFB in 2009 and 2004, respectively (Figure 2). In most years, the WSB activity exceeded that of DFB. From 1999 to 2019, 32.0% of Douglas-fir forests were affected by WSB, 18.4% were affected by DFB, and 9.5% experienced infestation by both WSB and DFB (Figure 1).

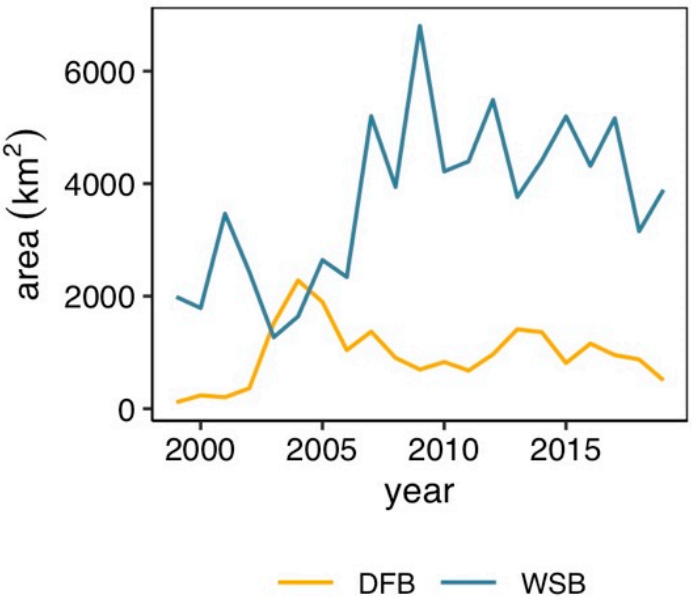

Figure 2. The annual area of Douglas-fir forest affected by Douglas-fir beetle (yellow) and western spruce budworm (blue) in the Southern Rocky Mountain ecoregion as reported in USFS ADS surveys for the Southern Rockies [25].

Across the study area, the cover of Douglas-fir varied widely (Figure 3). Most pixels with the presence of Douglas-fir were unaffected by DFB and/or WSB infestation in a typical year (Figure 1). Given the presence of either WSB or DFB within a pixel, WSB was generally more widespread than DFB; the median fractions of the area of a 960 × 960 m pixel with WSB and DFB were 0.32 and 0.063, respectively (Figure 3).

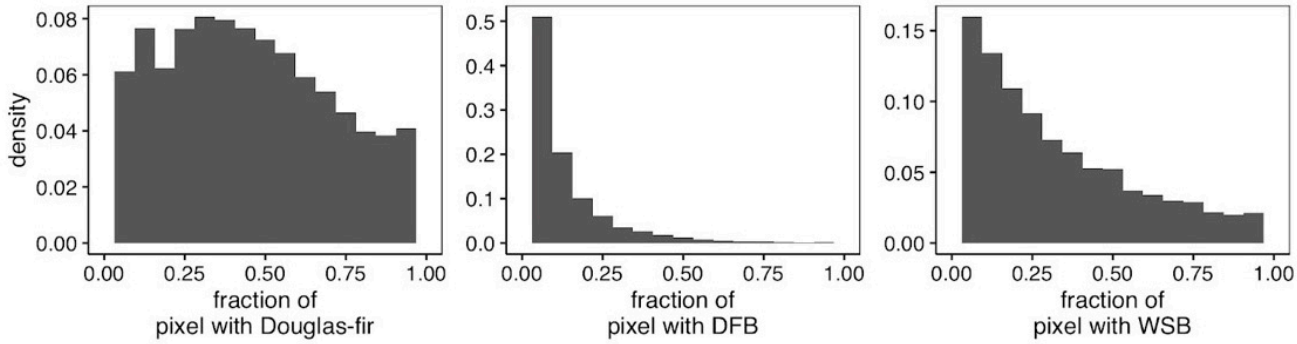

Figure 3. Histograms illustrating the density of observations by the fraction of 960 × 960 m pixels with Douglas-fir, Douglas-fir beetle, or western spruce budworm present, given each was present in the pixel. For DFB and WSB, distributions represent all years combined. Note that y-axes are on different scales to allow for easier interpretation of each panel.

The spatial overlay analysis demonstrated that DFB outbreak was preceded by WSB outbreak more frequently than was expected under a random spatial distribution (Figure 4). The strongest correlation was observed when WSB was present five years before the DFB presence (Figure 4). Of the 457,900 ha affected by both WSB and DFB, 63% (288,000 ha) experienced WSB outbreak prior to DFB, <1% (3400 ha) experienced WSB and DFB in the same year, and 34% experienced DFB outbreak prior to WSB. Stands affected by WSB 2–10 years prior (i.e., negative lags) were more than twice (range 2.2×–4.0×) as likely to experience DFB outbreak than expected. The concurrent activity of WSB and DFB occurred less frequently than expected (i.e., lag 0), but the difference was minimal. The area affected by both WSB and DFB in the same year was 230 ha less than expected. WSB followed DFB at rates that were, on average, 1.15× (range 0.97×–1.4×) greater than expected (i.e.,

positive lags). These findings are broadly consistent with the results from analyses that used different thresholds to define presence (Appendix A, Figure A1), analyses that used only ADS polygons where the focal host was listed as Douglas-fir (Appendix A, Figure A3), and analyses that used only ADS polygons where disturbance severity was listed as severe for WSB and low-moderate for DFB (Appendix A, Figure A5).

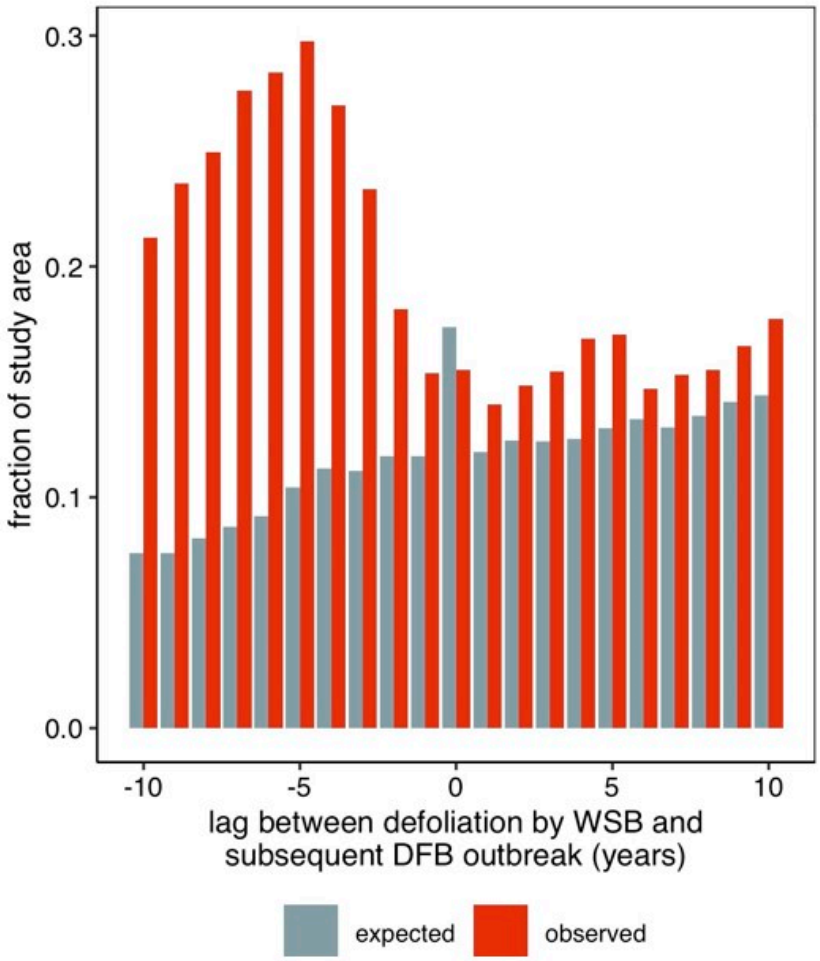

Figure 4. The observed and expected proportion of pixels affected by DFB and WSB by temporal lag. Negative values on the x-axis indicate that WSB defoliation occurred prior to DFB outbreak, whereas positive values indicate that WSB defoliation occurred after DFB outbreak; absolute values on the x-axis give the number of years (i.e., lag) between outbreaks of the two species. Red bars that exceed the height of grey bars indicate that spatiotemporal overlap of the two biotic agents occurs more often than expected due to chance at a given lag.

4. Discussion

Here, we demonstrate that prior defoliation by WSB increases the likelihood that Douglas-fir forests will experience subsequent outbreaks of DFB. This supports the hypothesis of reduced vigor in defoliated trees facilitating secondary disturbance and suggests a mechanistic linkage between WSB and DFB. Our findings corroborate localized field studies that demonstrate that prior defoliation by the Douglas-fir tussock moth may lead to increases in DFB populations [49] and the colonization of heavily defoliated trees [50]. Notably, our data suggest that the effect of prior defoliation on subsequent DFB outbreaks persists at broad spatial scales, despite complex cross-scale interactions that characterize bark beetle outbreaks [30]. Further, our data provide evidence for the linked effects of WSB defoliation being a likely contributor (along with other disturbances, such as drought and fire activity) to a trend of increasing DFB-caused tree mortality in the western USA [51].

Our results suggest that defoliation 2–10 years prior dramatically increases the probability of subsequent DFB outbreak. This time lag is consistent with studies of radial growth, which show that heavy defoliation by WSB often causes reductions in growth that may persist for a decade [27]. While radial growth has been widely used as an indicator of tree vigor and susceptibility to insect attack [52], recent research highlights the complexity of carbon-restricted trade-offs between growth and defense [12]. A better understanding of the growth–defense trade-offs that exist at the tree-scale and how these effects scale across time and space is essential to predicting future interactions among biotic disturbance agents.

While our results support a mechanistic link between tree defoliation and bark beetle infestation, previous research suggests that common stand drivers may also lead to overlap. Both WSB and DFB preferentially attack older stands [53] and may be facilitated by drought events [54,55]. These and other common drivers (e.g., stand composition) may explain why WSB presence was occasionally observed after DFB presence in our study. However, periods of above average moisture may benefit defoliators [54], and while both DFB and WSB target large trees, WSB also targets small trees [26]. Additionally, in some cases, combined WSB defoliation and drought may lead to decreases in phloem diameter that are severe enough to deter bark beetle infestation [30]. Therefore, the overlap in drivers may not be significant enough to explain our findings. More research is needed to understand the relative influences of shared drivers vs. the mechanistic effects of defoliation on trees' susceptibility to subsequent infestation. Nonetheless, our results describing different sequences and lag times between outbreaks of defoliators indicate that mechanistic effects may be important in driving the overlap of WSB and DFB.

We took a conservative approach to account for several known limitations of the spatial datasets, as well as to assess the sensitivity to subjective decisions made throughout our analyses. For example, the ADS geospatial data and host cover data have potential measurement and classification errors due to variable flying and viewing conditions and differences among the interpretations of individual surveyors. However, assessments of USFS ADS data have found a high accuracy in identifying damage type and tree genera, with an 87% accuracy for tree species, 79% accuracy in damage location for bark beetles (spatial tolerance of 500 m), and 70% accuracy in identifying the damage agent species [41,45]. Though there is relatively high accuracy in the survey data, we conservatively classified the insect presence, aggregated survey data to a coarse resolution to account for locational error, and confirmed that our results were relatively insensitive to variations in analytical procedures (Appendix A, Figures A1, A3 and A5).

Knowledge of disturbance interactions, particularly prior disturbances that facilitate subsequent disturbances, is needed to inform adaptive management in forest ecosystems and to develop more detailed projections of future dynamics [19]. Modern forest management requires careful consideration of societal needs and ecological processes [56], and our research addresses a key linkage between two ecological processes that affect a widely distributed and economically valuable tree species. Our results indicate that forest managers should be aware that elevated DFB populations are likely to be found in stands with recent (previous ca. 2–10 years) impacts of defoliation by WSB, with outbreaks most likely to occur five years after WSB presence. To the largest extent possible, these linked disturbances and feedback mechanisms should be incorporated into ecological models used to project future changes in forest dynamics. Further study investigating the effect of WSB defoliation severity on subsequent DFB outbreak is needed to deepen our understanding of this interaction.

5. Conclusions

Warmer and drier conditions due to climate change are expected to increase WSB and DFB activity in many forests throughout the western United States, independent of any mechanistic linkage between these two insects. This has important consequences for the persistence of forest communities by influencing tree vigor and mortality. Our study of the linkage between WSB outbreak and subsequent DFB outbreaks in Douglas-fir forests

suggests that tree mortality may increase due to the effects of WSB on host susceptibility to DFB infestation. Effects from such disturbances may have consequences for the stand structure and may impact forest ecosystems via altered energy and nutrient cycles. Because Douglas-fir forests span extensive areas throughout western North America and provide many ecosystem services, knowledge and consideration of such biotic disturbance agent interactions are essential for predicting climate-mediated forest changes and managing forest resources.

Author Contributions: Conceptualization, S.J.H., H.M.C. and N.J.T.; methodology, S.J.H., H.M.C. and N.J.T.; formal analysis, S.J.H. and H.M.C.; writing—original draft preparation, H.M.C. and S.J.H.; writing—review and editing, R.A.A., K.C.R., N.J.T., C.B., A.W., O.S., H.M.C. and S.J.H. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Data are all publicly available through the USDA Forest Service Geodata Clearinghouse (https://data.fs.usda.gov/geodata/), which was last accessed on 3 June 2021.

Conflicts of Interest: We declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A

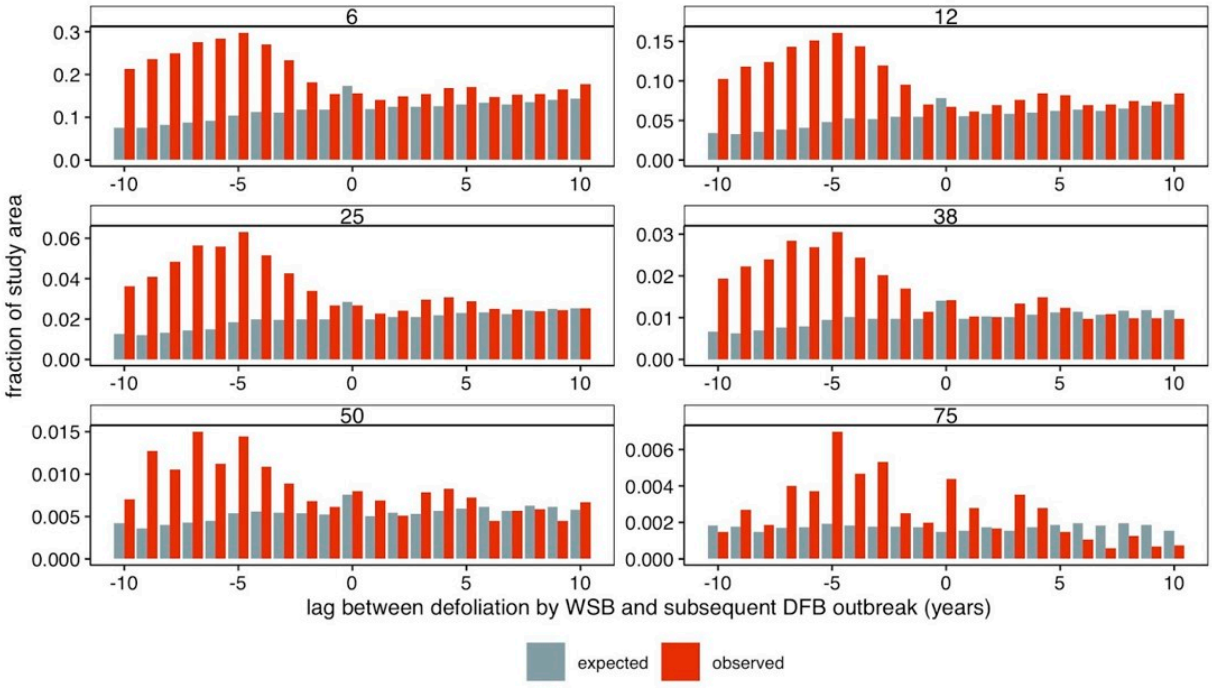

Figure A1. The observed and expected proportion of pixels affected by DFB and WSB by temporal lag for several thresholds (6%, 12%, 38%, 25%, 50%, 75%; panels) of percent area used to define the presence of DFB, WSB, and Douglas-fir. Here, −5 signifies that WSB defoliation occurred 5 years prior to DFB presence. Note that y-axes span different ranges.

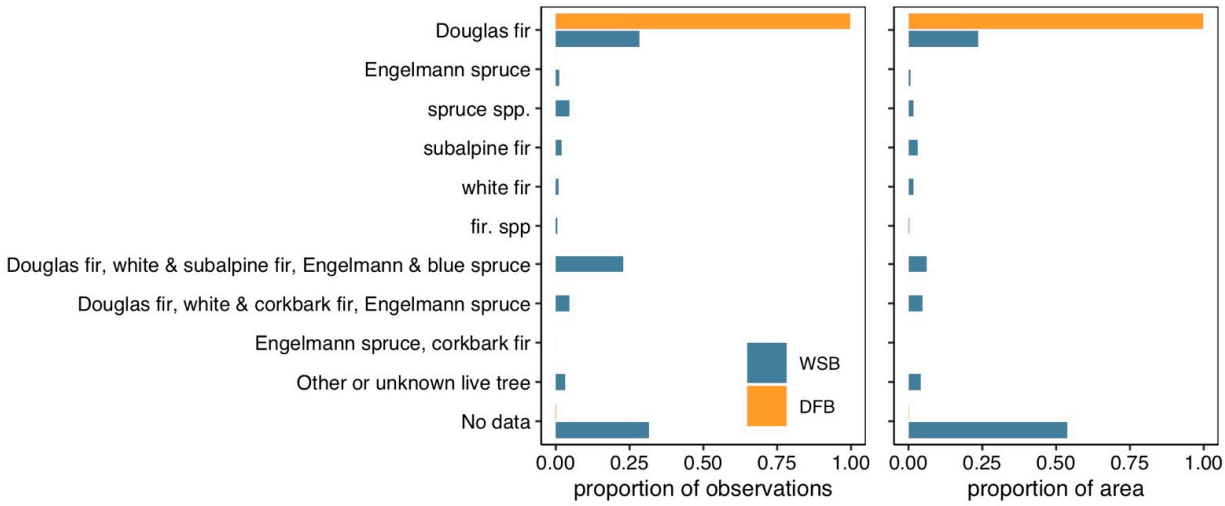

Figure A2. The proportion of ADS observations and area of ADS polygons by host identity and primary damage causing agent. In USFS Region 3, which includes New Mexico, only host groups (e.g., Douglas fir, white and subalpine fir, Engelmann and blue spruce) were recorded over the study period.

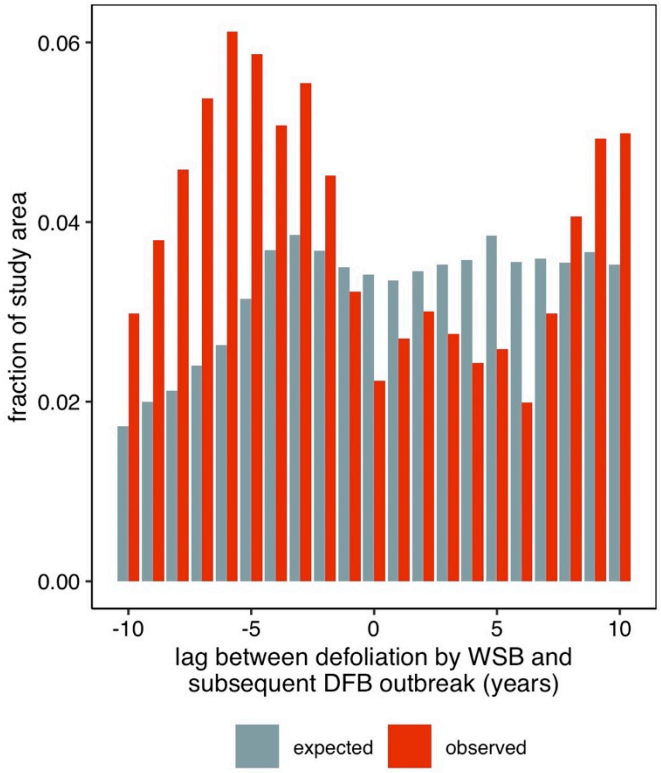

Figure A3. The observed and expected proportion of pixels affected by DFB and WSB by temporal lag for only pixels where the USFS Aerial Detection Surveys listed the Douglas-fir as the primary host and at least 25% (a four or more 240 × 240 m subpixel) listed presence of the agent. Here, −5 signifies that WSB defoliation occurred 5 years prior to DFB presence. Red bars that exceed the height of grey bars indicate that spatiotemporal overlap of the two biotic agents occurs more often than expected due to chance at a given lag.

Over the study period, USFS ADS teams have estimated damage severity using several different methods. Prior to 2012, the severity of tree mortality was estimated as either the number of trees killed per polygon or the density of trees killed (i.e., trees per acre). More recently, surveyors have recorded disturbance severity using five broad

categories (e.g., very light (1–3%) or moderate (10–30%). To harmonize these different data collection methods, we followed approaches outlined by Egan et al. (2019) [57] and Hicke et al. (2020) [1]. Specifically, we converted estimates of the number of killed trees to a density and then classified the density of tree mortality into three categories, based on comparisons between field and ADS data [57]. We then collapsed the five-class system so that it aligned with the three-class system. Finally, we repeated overlay analyses for only ADS polygons where stand-level defoliation was severe (>50%) and bark beetle severity was low-moderate (<30%), based on the assumption that severe defoliation may trigger DFB outbreak development.

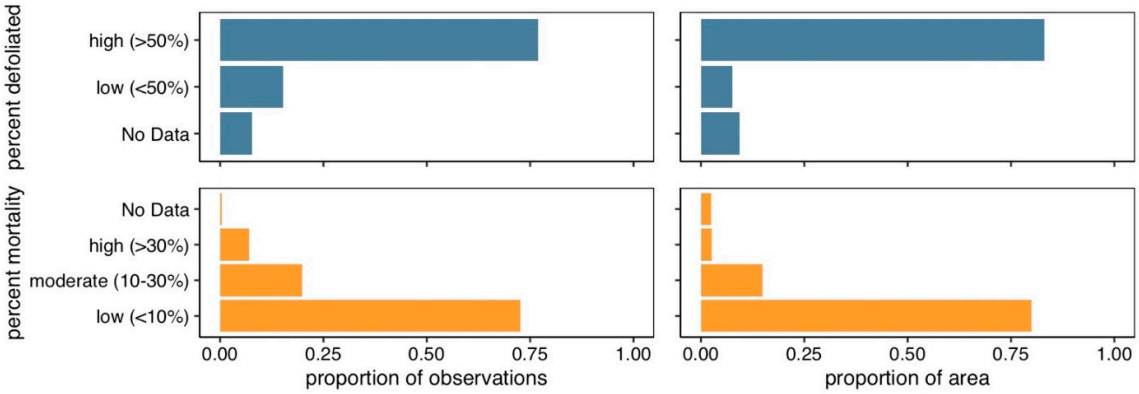

Figure A4. The proportion of ADS observations and area of ADS polygons by damage severity, characterized by percent defoliated for WSB (**top**) and percent mortality for DFB (**bottom**).

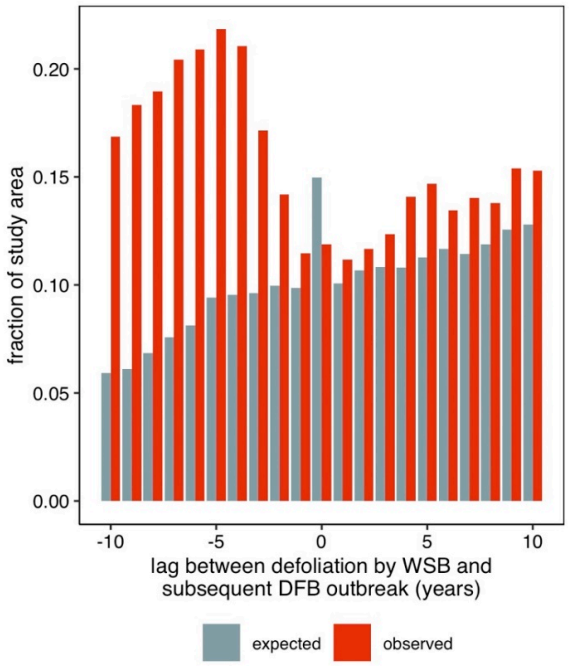

Figure A5. The observed and expected proportion of pixels affected by DFB and WSB by temporal lag for only pixels where the USFS Aerial Detection Surveys listed the severity of DFB-attributed tree mortality as low-moderate and WSB-attributed defoliation severity as high. Presence is defined as at least 25% (a four or more 240 × 240 m subpixel) listed presence of the agent and host. Here, −5 signifies that WSB defoliation occurred 5 years prior to DFB presence. Red bars that exceed the height of grey bars indicate that spatiotemporal overlap of the two biotic agents occurs more often than expected due to chance at a given lag.

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