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REVIEW ARTICLE

Putting more fuel on the fire… or maybe not? A synthesis of spruce beetle and fire interactions in North American subalpine forests

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Abstract
Context Disturbance interactions can create compound, novel effects across landscapes compared to individual disturbance events. However, little consensus exists regarding which mechanisms are important for controlling the interaction of two disturbances with similar climatic forcings in subalpine spruce–fir forests.
Objectives To investigate the importance of controls on disturbance interactions, we first outline potential mechanistic links between spruce beetle outbreaks and fires based on existing research. Second, we update the theoretical framework used to understand interactions between spruce beetles and fire in subalpine spruce–fir forests. Third, we provide expectations for potential interactions and suggest avenues for further research.
Methods We synthesized existing primary literature to categorize the potential mechanisms controlling the interactions between spruce beetles and fire.
Results We categorized mechanisms as either substrate mediated or environmentally mediated. Most research investigating the interaction between spruce beetle outbreaks and fire focuses on substrate mediation. There is a need to expand investigations of environmental mediating mechanisms due to the importance of climate and the ability for either disturbance to alter microclimatic conditions.
Conclusions Environmentally mediated mechanisms may better elucidate the interactions between spruce beetles and fire than substrate mediated mechanisms because both disturbances require specific environmental conditions, and both can alter environmental conditions that favor a second disturbance. Our understanding of how these mechanisms promote or constrain interactions is limited and warrants future study. Investigating these topics and expanding the scope of research both spatially and temporally may identify additional patterns that increase the predictability of this important disturbance interaction.

Keywords Compound · Disturbance · Fire · Interaction · Short-interval · Spruce beetle (*Dendroctonus rufipennis*)

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Introduction

Disturbances shape the structure and composition of forest communities (Oliver 1980; Bazzaz 1983; Harvey et al. 2016; Seidl et al. 2016). Climate driven disturbances (e.g., fire, drought, insects) are likely to change substantially in frequency, severity and/or extent as a result of anthropogenic

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warming (Seidl et al. 2017) and may consequently lead to unprecedented alterations to forest structure and composition (Turner 2010; Andrus et al. 2021; Hayes and Buma 2021). These alterations are due in part to the emerging characteristics of more frequently overlapping and interacting disturbance events (Buma 2015). Disturbance interactions can lead to nonlinear and novel effects, such that both disturbances in combination create compound changes to forest structure and composition that are unique from either independent disturbance event (Buma and Wessman 2011; Hansen et al. 2016; Dobor et al. 2020). When investigating disturbance interactions, it is important to consider the ability of a first disturbance to alter the conditions needed for a second disturbance, especially in ecosystems characterized by multiple severe disturbance events.

Disturbances in North American subalpine forested ecosystems occur across a spatial–temporal gradient from relatively frequent avalanches occurring within spatially-confined hillslopes to infrequent and severe spruce beetle epidemics, fires, and wind-throw events occurring across landscapes (Baker and Veblen 1990; Rebertus et al. 1992). Subalpine spruce–fir forests in western North America are of special importance due to their limited capacity to resist severe disturbance events, as demonstrated through slow regeneration or altered trajectories following fire and/or spruce beetle outbreaks (Schoennagel et al. 2004; Sibold et al. 2006; Raffa et al. 2008; Windmuller-Campione and Long 2015). In this study, we focus on two principal disturbances in North American subalpine spruce–fir ecosystems: fire and spruce beetle epidemics. Together, fire and beetle outbreaks comprise the majority of disturbed area in subalpine spruce–fir forests in western North America (e.g. fire, 1986–2010: 2–4%; beetles, 1997–2010: 6–11%; harvest, 1986–2010: 5–8% of total forest area in Pacific Northwest, Gu et al. 2016). Importantly, both are sensitive to climate change effects in similar ways—warmer, drier conditions favor both (Barrows 1951; Schmid and Frye 1977), creating the expectation that both will increase in frequency in the future (Derose and Long 2012). However, little consensus exists regarding the interactions between these disturbances which likely arises from our limited understanding in the ability of a first disturbance to modify the conditions needed for a second disturbances.

Both fire and spruce beetles have been investigated thoroughly as individual disturbance agents in subalpine spruce–fir forests. Fire in particular is a primary disturbance event in subalpine spruce–fir forests. These systems typically burn severely but infrequently (mean fire return interval = 202 years; Colorado: Veblen et al. 1994). Long periods between fires result from cool and moist climates at high elevations, lowering ignition and spread probabilities, and allowing for substantial fuel build up between events (Bessie and Johnson 1995). Because fire occurrence depends in part on appropriate climatic conditions, recent prolonged drought and increasing annual temperatures in western North America (Harvey et al. 2016) have enabled more frequent fires and larger areas burned (Hansen et al. 2020). Fires under extreme climatic conditions can cause widespread complete canopy mortality and therefore an almost complete loss of forest structure (Romme 2012), which together with a warming climate has substantial implications for forest recovery. Removing overstory tree species via increased fire alters local energy budgets (Reed et al. 2016) and reduces subsequent seed sources (Andrus et al. 2021; Schapira et al. 2021), both of which have the potential to delay post-fire regeneration of subalpine forests to pre-disturbance conditions for centuries (Bebi et al. 2003), or indefinitely (Calder and Shuman 2017; Calder et al. 2019; Coop et al. 2020).

Alongside fire, native spruce beetles are another significant agent of mortality with the ability to change forest structure (Hopkins 1909; Schmid and Hinds 1974; Baker and Veblen 1990; Veblen et al. 1991; Diskin et al. 2011; Derderian et al. 2016; Rodman et al. 2021). Specific to North America, the dominant bark beetle in subalpine spruce–fir forests is the spruce beetle (*Dendroctonus rufipennis*), which also responds to changes in climate by altering its population dynamics (Coulson 1979; Vega and Hofstetter 2015). Smaller, stable populations are generally only capable of killing old, damaged, and already dying trees (Schmid and Frye 1977). However, warmer and drier winters allow spruce beetle populations to grow from background level populations into epidemic-level numbers (Coulson 1979). These shifts in population dynamics create outbreaks on the scale of millions of hectares and paired with increasing summer drought and tree stress cause wide scale forest mortality (Raffa et al. 2008). While both spruce beetles and fire are altered by warming and drying climate, unlike fire, spruce beetles are highly host-specific and have a proclivity for larger diameter host trees (Holsten et al. 1999). Spruce beetle mortality does not completely remove overstory structure and increases structural complexity after the disturbance (Parish et al. 1999). Additionally, bark beetle disturbances cause mortality over multiple years (Hyde et al. 2016) which can affect the response of the legacy community (Pappas et al. 2020).

This literature review examines potential mechanisms that control the interaction between fire and spruce beetle outbreaks, two related yet distinct disturbances. There is a growing recognition that disturbance events interact with prior legacies to produce novel results on forest structure and composition (Buma 2015; Burton et al. 2020). Thus, understanding the mechanisms that control the interactions between infrequent disturbances with similar climatic triggers and return intervals that cause widespread mortality and that may preclude future forest regeneration is paramount for the future of these forests. Here, we use the definition of disturbance interactions according to Buma (2015), focusing on mechanistic feedbacks between post-disturbance legacies and subsequent disturbance processes that result in substantive changes in the likelihood and magnitude (e.g., smaller fires; linked disturbances), or ecological severity (e.g., altered resilience; compound disturbances) of subsequent disturbance events. Several researchers have asked questions related to the mechanisms of interactions between fires and spruce beetles in western North American forests (Table 1), primarily to understand the outcomes of the interaction. To our knowledge, no study has synthesized the various disparate studies to understand the consensus or importance of a first disturbance for altering the conditions needed for a second disturbance. The purpose of this literature review is to (1) outline potential mechanistic links for the interactions between spruce beetle outbreaks and fire events based on existing research, (2) update the theoretical framework and paradigm used to understand interactions between the closely related mountain pine beetle and fire in upper montane and subalpine forests for spruce beetles and fire in subalpine spruce–fir forests, and (3) provide baseline expectations for potential interactions and suggest avenues for further research.

Existing research

We used Scopus, an online citation database for scholarly articles, on 4/12/2021 to identify previous literature on spruce beetle and fire interactions. We searched for articles that contained the terms 'spruce beetle', 'fire' with a third term, either 'compound', 'interaction', or 'short interval' that we varied to increase the potential number of articles retrieved. We varied our third term due to differences in terminology within the published literature and to assess if the literature adequately captures the potential or reality of disturbance interactions and subsequent, cascading effects on future disturbances. Our search yielded 32 documents that included these terms. Of the 32 documents, 7 were on different insect species and 1 did not directly research more than 1 disturbance within the paper. The 24 remaining papers contained both fire and spruce beetle interactions in spruce–fir forests in western North America. We then examined the citations within these 24 papers to identify literature that we missed within our initial search. We identified 1 new paper for a total of 25 papers (Table 1; Fig. 1). We traced mechanisms through other literature (e.g., the hydrological literature) as they revealed themselves in our initial survey. We excluded adjacent literature reviews (e.g., McCullough et al. 1998, Negrón et al. 2008, Black et al. 2013, Kane et al. 2017) and book chapters (e.g., Furyaev et al. 1983, Knight 1987, Peet 2000, Veblen 2000, Kulakowski and Veblen 2015) from our review that focus on the mountain pine beetle and lodgepole pine systems. Although the impacts of mountain pine beetle on lodgepole pine are well studied, they represent a different system with different fire regimes and disturbance limitations. However, these reviews are conceptually valuable summaries of existing research on bark beetle and fire dynamics in other systems. The topic of spruce beetle and fire interactions has received more attention in peer reviewed literature within the last 5 years, with 36% of the 25 documents published between 2016 and 2021 (average of 1.8 document per year). The other 64% of the 25 documents span 25 years between 1990 and 2015 (average of 0.64 documents per year).

Table 1 Mechanisms for the interaction between spruce beetles and fire in subalpine forest

Publication	Mechanism	Interaction direction	Time from last disturbance and investigation	Methods
Baker and Veblen (1990)	N/A	Documentation of SB and fire	Variable	Photo analysis
Veblen et al. (1994)	Substrate mediated	Fire interacts with SB	Variable	GIS; field sampling; dendrochronology
Howe and Baker (2003)	Substrate mediated	Fire interaction with SB	540−90 years	Aerial detection; field sampling; GIS; dendrochronology
Bebi et al. (2003)	Substrate mediated	Fire interacts with SB SB does not interact with fire	61 years	Field sampling
Hart et al. (2014)	Substrate mediated	Fire does not interact with SB	170 years	Field sampling
Temperli et al. (2015)	Substrate mediated	Fire interacts with SB	–	In silico
Kulakowski et al. (2016)	Substrate mediated	Fire interacts with SB	61 years	Field sampling; dendrochronology
Bakaj et al. (2016)	Substrate mediated	Fire interacts with SB	61 years	GIS; field sampling; dendrochronology
Bigler et al. (2005)	Resource mediated; potentially Env condition mediated	SB interacts with fire probability	< 3 years	Spatially explicit modeling
Kulakowski and Veblen (2007)	Substrate mediated	SB does not interact with fire extent or severity	< 5 years	Dendrochronology; aerial photograph interpretation; field sampling; GIS
Jenkins et al. (2008)	Substrate mediated	SB interaction with fire	140–0 years	Review; in silico
DeRose and Long (2009)	Substrate mediated	SB interacts with crown fire probability	10–20 years	Field sampling; FVS simulation
Makoto et al. (2012)	Substrate mediated	SB interacts with charcoal production	1 year	Field sampling
Page et al. (2014)	Substrate mediated	SB interacts with foliage flammability	0–14 months	Aerial detection; field sampling
Hansen et al. (2016)	Substrate mediated	SB interacts with fire likelihood	< 2 years	GIS
Mietkiewicz et al. (2018)	Substrate mediated	SB interaction with fire	75–5 years	Dendrochronology; field sampling
Carlson et al. (2017)	Substrate mediated	Compound interaction between SB and fire	< 1 year & 2 years	Landsat; field sampling
Andrus et al. (2021)	Substrate mediated	Compound interaction between SB and fire	1 year & 6 years	Field sampling
Schapira et al. (2021)	Substrate mediated	Compound interaction between SB and fire	1–3 years	Aerial detection; field sampling
Parish et al. (1999)	Environmental condition mediated	SB control stand dynamics in the interfire period	140–94 years	Dendrochronology
Kulakowski et al. (2003)	Environmental condition mediated	Fire interacts with SB	60 years	Field sampling; dendrochronology
DeRose and Long (2012)	Environmental condition mediated	Drought mediates interactions of fire and SB	400–5 years	Aerial detection; field sampling; dendrochronology

Table 1 (continued)

Publication	Mechanism	Interaction direction	Time from last disturbance and investigation	Methods
Andrus et al. (2016)	Environmental condition mediated	No interaction between fire and SB	1–2 years	Field sampling
Carlson et al. (2021)	Environmental condition mediated	SB interacts with fire	10–15 years	GIS; field sampling

A description of the interaction effects documented in each paper are presented in Appendix A of the Online Supplementary Material. The table is sorted by interaction direction, then mechanism, then year published

[a]Research was conducted on the Kenai Peninsula of AK. Although the Kenai Peninsula is comparable to subalpine spruce–fir forests it is not identical

Identifying mechanisms of spruce beetle–fire interactions

We identified two mechanistic categories—substrate mediated vs. environmental conditions mediated—responsible for the interaction between spruce beetles and fire (Table 1). Using the primary line of questioning within each article, we categorized whether a study focused on physical substrate or resource (e.g., host trees for spruce beetles or fuels for fires) as a mechanism or the environmental conditions required to support either of the disturbances (i.e., micro and macro climatic conditions). We use the term "substrate" to generalize across fire fuels and host trees, bypassing using the term 'resources' to avoid referring to other materials important to plant growth but not relevant for beetles or fire. We also discuss the direction and effect of the interaction given the variation within the literature (full description of interaction effects in Online Appendix A).

Substrate mediated interactions

The linked interaction of fire on subsequent spruce beetle outbreaks

Fires alter the food substrate available for spruce beetle populations. Within the literature surveyed, 32% of papers (8 of 25) investigated the interaction between fire events and subsequent spruce beetle disturbances (Table 1). High severity fire events that precede spruce beetle outbreaks decrease the extent and severity of future spruce beetle outbreaks (Veblen et al. 1994; Bebi et al. 2003; Temperli et al. 2015; Bakaj et al. 2016; Kulakowski et al. 2016) by causing mortality in appropriately sized host trees (*Picea* spp. > 46 cm DBH; Holsten et al. 1999) across a landscape. The duration of this interaction is determined by the time spruce trees take to regenerate to appropriate sizes and to serve as adequate habitat for spruce beetles (Hart et al. 2014). Spruce regeneration is mediated through local productivity processes (climate, nutrients, etc.) but can take over 100 years to reach size classes predominantly predated by spruce beetles (Veblen et al. 1994). The extent of low severity fires in the subalpine may be positively correlated with the extent and severity of subsequent spruce beetle outbreaks because fire events that do not cause mortality are likely to weaken and damage trees and increase suitable substrate for future spruce beetle outbreaks. However, low severity fires in the subalpine are atypical (Sherriff et al. 2001). Thus, historically, high severity fires reduce beetle outbreaks in the short term, though they may synchronize landscapes for later outbreaks (Kulakowski et al. 2016); low severity fires remain an open question.

The linked interaction of spruce beetle outbreaks on subsequent fires

Spruce beetle outbreaks may modify subsequent fire characteristics as well via changes in fuel substrates. Most of the literature surveyed for this scenario highlights substrate mediation through investigations into changes in fuel structure or availability (9 out of 11 papers investigating spruce beetle interaction with fire in Table 1). However, individual studies often focus on different aspects of fuel. Research conducted by Page et al. (2014) observed spruce beetle-induced increases to Engelmann spruce foliage flammability

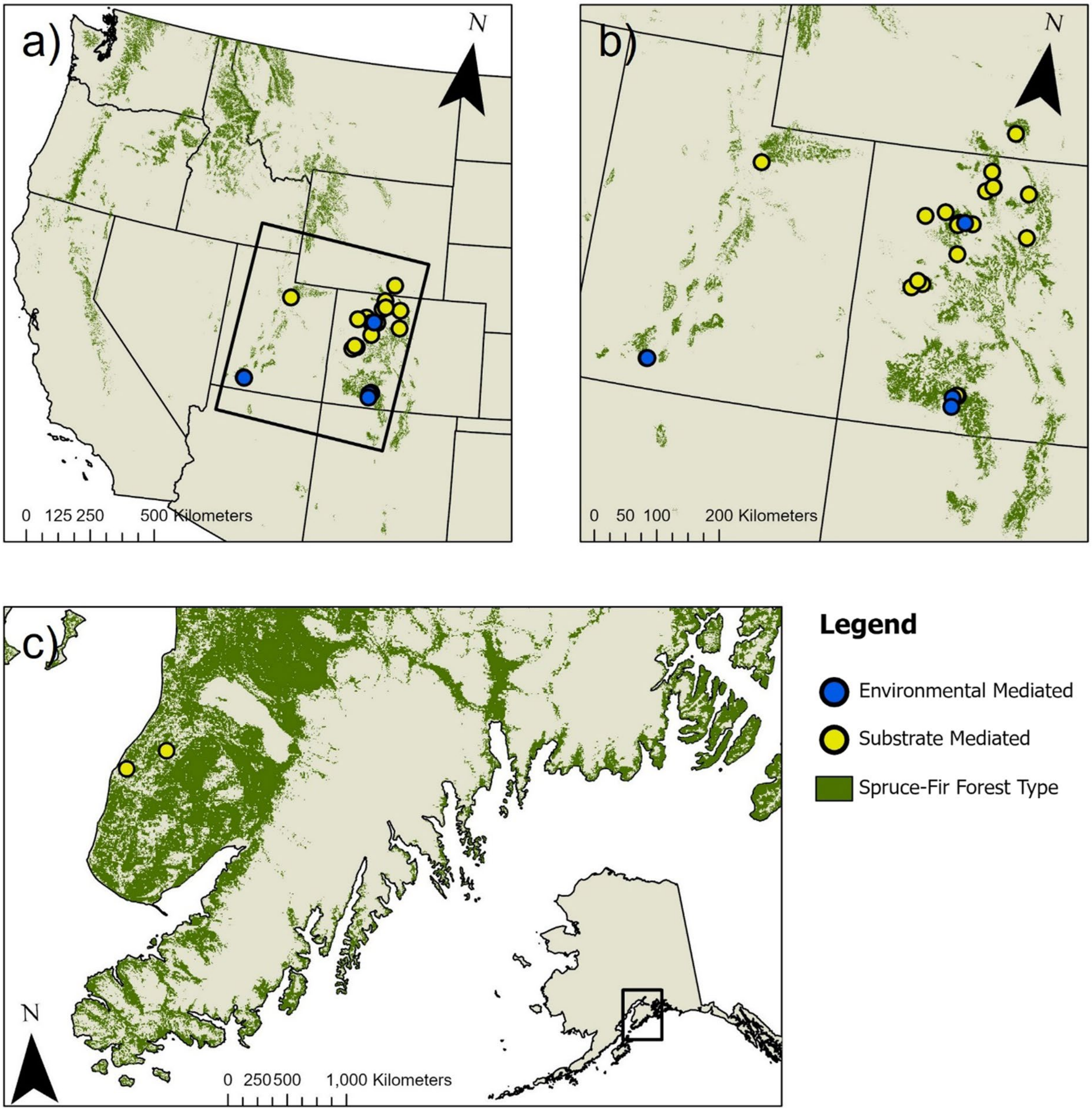

Fig. 1 Map of study locations included in Table 1. Points have been differentiated by color based on the mechanisms investigated within the literature. Spruce–fir forests have been identified at a landscape scale, thus the specific species composing these forests varies across latitude

within a year of the beetle outbreak, potentially leading to increased crown fire potential in recently attacked stands. However, after needle drop (> 1 year) the direction of the interaction inverses. Derose and Long (2009) investigated the crown fire potential of spruce beetle attacked stands over longer time scales using simulations guided by field measurements and concluded that overall crown fire potential decreases due to a reduction in crown fuels. Other research conducted by Bigler et al. (2005) observed slight increases in the probability of high severity fire, likely due to greater abundances of fuels of a variety of sizes. Alternatively, Kulakowski and Veblen (2007) observed fire extent and severity to be independent of historic spruce beetle outbreaks. Many of these investigations occur across disparate time scales (Table 1) with unclear comparisons between the time between spruce beetle outbreak and fires and the time between the most recent disturbance and investigation making generalizable conclusions about the interaction effect of spruce beetle outbreaks on subsequent fires difficult.

The compound interaction of spruce beetle outbreaks followed by fire events

Recent investigations (within the last 4 years; 2017–2021) explicitly pursue questions related to the compound effects of both disturbances on forest regeneration to pre-disturbance structure and composition. We classify these investigations as substrate mediated because both disturbances work in combination to limit the resources needed for forest recovery (i.e., decreases in locally available seed sources of pre-disturbance dominant trees). Within the literature surveyed, there only appear to be studies on the effects of spruce beetle outbreaks followed by fires on forest regeneration. No investigation evaluates the compound interaction of fire events followed by spruce beetle interactions, likely due to the inability of post-high severity fire stands to support spruce beetle outbreaks and the infrequent occurrence of low severity fires in this system. The compound effect of spruce beetle outbreaks followed by fire has been observed to be associated with greatly diminished vegetative recovery such that the severity of spruce beetle outbreak was negatively correlated with post-fire vegetation recovery as defined by comparisons using a normalized difference vegetation index (NDVI; Carlson et al. 2017). Importantly, the negative correlation of vegetation recovery with spruce beetle outbreak severity was stronger during time periods where trees had not dropped their needles (red phase) compared to time periods where trees had dropped their needles (grey phase). This interaction effect could be moderated through short term increases in needle flammability following spruce beetle outbreak that diminishes over time as trees drop their needles (Page et al. 2014). Additionally, research conducted by Andrus et al. (2021) observed lower regeneration densities of the pre-disturbance dominant spruce. They suggest that spruce beetle outbreaks reduce available seed trees then subsequent fires further reduce seed availability of spruce trees and allow for forest composition to trend towards wider dispersing species like aspen. Alternatively, Schapira et al. (2021) did not observe a significant difference in seedling densities between stands that experienced either spruce beetle outbreak followed by fire or fire alone.

Environmental conditions mediated Interaction

Many papers discussed prior acknowledge the importance of climate in subalpine fire dynamics (e.g., Bebi et al. 2003, Jenkins et al. 2008, Kulakowski et al. 2016); however, the role of environmental conditions as a mechanism linking spruce beetles and fire is not explicitly investigated within these papers. Within the literature surveyed, only 20% of papers (5 of 25) explicitly investigate the effect of one disturbance influencing the environmental conditions as a mechanism for the second disturbance (Table 1). Both fire and spruce beetle outbreaks require specific macro- and micro-climatic conditions to occur (Derose and Long 2012). Spruce beetles and fire are both independently capable of altering microclimate conditions such that post fire environments are associated with increases in subcanopy temperature while post spruce beetle environments are associated with decreases in subcanopy temperatures (Carlson et al. 2021). Additionally, spruce beetle outbreaks can decrease canopy sublimation and alter the hydrologic budgets of forests such that snowpack increases significantly (Frank et al. 2019). Spruce beetle outbreaks, and the cool and wet environments that follow, have been hypothesized to be the determinant of forest composition and structure during inter-fire periods in subalpine spruce–fir forests (Parish et al. 1999) and may further reduce the susceptibility of stands to subsequent low-severity fires (Kulakowski et al. 2003). There are additional instances within the hydrology literature that demonstrate how fires (e.g., Harpold et al. 2014; Gleason and Nolin 2016) and spruce beetle outbreaks (e.g., Frank et al. 2019; Manning et al. 2021) independently influence the microclimatic conditions necessary for a second disturbance. Fires tend to increase snowmelt rates caused by charred trees that reduce snow albedo (Gleason and Nolin 2016) and decrease the volume of snow water available to melt when compared to unburned forests (Harpold et al. 2014). In contrast, spruce beetles tend to increase snowpacks by reducing canopy sublimation (Frank et al. 2019) as well as increase streamflow post outbreak (Manning et al. 2021). Unfortunately, those studies do not extend to the likelihood or impact of a second disturbance explicitly, and so can provide suggestions and hypotheses for the linked disturbance interactions but not specifics. Importantly, the importance of the alterations to environmental conditions on their subsequent effects on the interaction between these two disturbances remains broadly unresolved.

Updating the theorical framework for spruce beetles

Untangling the interactions between spruce beetles and fire requires developing an appropriate theoretical framework to guide future research and to clarify existing uncertainties. Current research is limited and primarily investigates substrate mediation through resources—appropriately sized host trees for beetles and change in fuel structure for fires—as the mechanism linking the two disturbances (Fig. 2). Substrate constraints (e.g., fuels for fire) are an important aspect of subsequent disturbance severity and extent (Bessie and Johnson 1995; Schoennagel et al. 2004), thus the predominant focus in the literature on the role of disturbance substrate is understandable. However, consensus across studies depends on the direction of the interaction. When fire is the first disturbance and succeeded by spruce beetle disturbance, the removal of appropriately sized host trees limits the spruce beetle outbreak for a time (typically determined by tree regeneration and growth rates, Hart et al. 2014). This is supported by the consensus within the literature on the direction and effect of this interaction (Table 1; Online Appendix A). There is less consensus within the literature on the direction and effect of spruce beetle outbreaks that are followed by fires (Table 1; Online Appendix A). Much of the literature on this interaction investigates substrate mediation through fuels which is reminiscent of the framework for interactions between the closely related mountain pine beetle and fire (Hicke et al. 2012). Importantly, subalpine forested ecosystems are not thought to be fuel

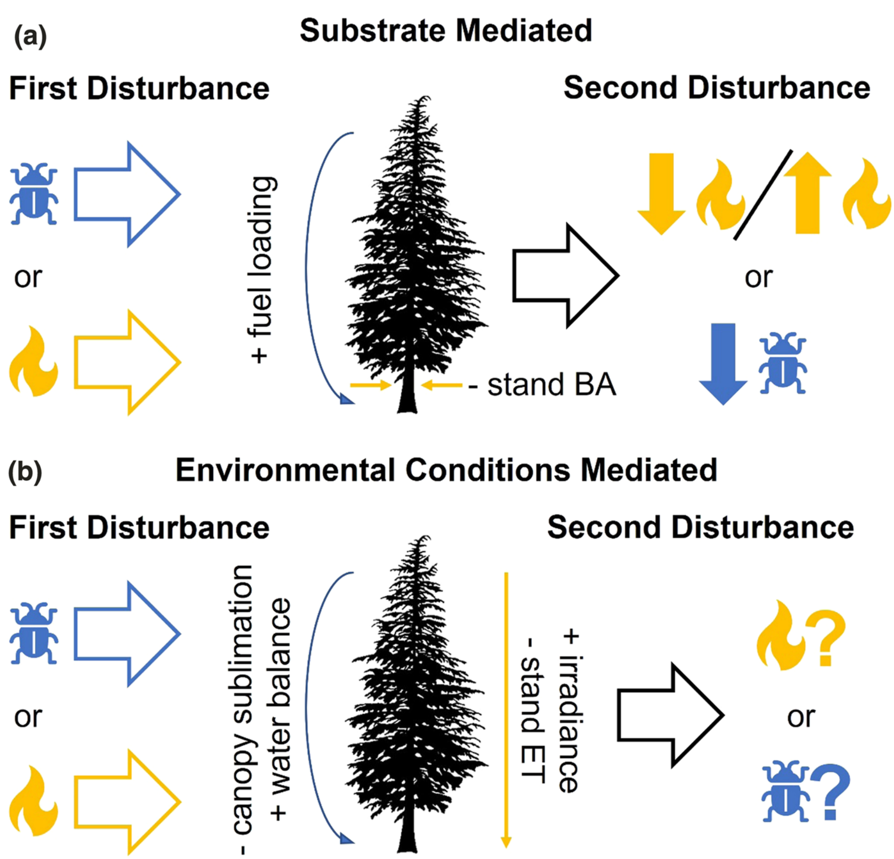

Fig. 2 Our proposed theoretical framework for future investigations of spruce beetle and fire interactions. Panel a illustrates that both spruce beetle outbreaks and fire have the potential to alter the substrate (fuel loading and stand basal area) needed for a second disturbance. The outcomes of this modification are not resolved within the literature for spruce beetle outbreaks that are followed by fire but are in clear consensus for fires that are followed by spruce beetle outbreaks. Panel b illustrates that both spruce outbreaks and fires are capable of modifying the environmental conditions [irradiance, evapotranspiration (ET), water balance, and sublimation] that are necessary for a second disturbance. However, little research has been conducted on this topic

limited during inter-fire periods (Sherriff et al. 2001); thus, changes in substrate structure following the spruce beetle outbreak are not likely to substantially influence future fires. Therefore, if there are significant interactions now (or which will emerge in future climates), it would be fruitful to investigate the other factors influenced by beetle mortality and which also influence fire.

New avenues for research

The underlying cause for inconsistent findings in studies investigating the interaction of spruce beetle outbreaks and subsequent fires suggests a need for more research. Specifically, investigations need to explicitly identify known influences of a first disturbance on environmental-mediating mechanisms (i.e., microclimate, water balance, etc.) and identify subsequent unknown influences these changes have on future disturbance interactions. This is imparted because similar macro-climatic conditions control both disturbances and because both disturbances have the capacity to alter microclimatic conditions (Fig. 2; Harpold et al. 2014; Gleason and Nolin 2016; Frank et al. 2019; Manning et al. 2021). We can improve our understanding of the interaction of fires and spruce beetles, regardless of interaction direction, by incorporating research investigating alterations to environmental conditions. Specifically, we suggest investigating environmental conditions that are likely to be altered by the first disturbance and can subsequently influence the likelihood of the second disturbance (either synergistically with warming climates or antagonistically). Some of this work can be leveraged from the hydrological community and other disciplines, although the explicit connection to the next disturbance is needed to answer the questions posed here. Such mechanisms are likely to be those that operate on a finer scale (i.e., fuel moisture or subcanopy temperature; Carlson et al. 2017). Although scaling and the effect size of this relative to macroclimatic drivers is unknown (with respective to subsequent disturbances), and worth investigating.

A potentially significant modification of local environmental conditions important for the interaction between spruce beetles and fire was identified by Frank et al. (2019). Their research showed a significant increase in snowpack 10 years after a spruce beetle outbreak in the Southern Rockies (Frank et al. 2019). Spruce beetles partially removed the canopy from spruce–fir forests which corresponded with a decrease in the sublimation of snowpack from the forest canopy and in turn significantly increased surface snowpack. This increase in moisture via snowpack corresponded to increases in soil moisture across the landscape (Frank et al. 2019) and has the potential to dampen conditions required for fires in systems with climatically limited fire regimes. Additional fuel moisture, independent of fuel quantity, may impede future fire characteristics, serving as a mechanism to alter the interactions between the disturbances. However, understanding how known shifts in microclimates influence disturbances interactions remains under-researched. Many questions remain, including: Do increases in snowpack significantly increase fuel moisture? Are small-scale increases in fuel moisture important for fire ignition and/or spread? How temporally persistent are shifts in microclimate? The increases in fuel moisture could act as a negative feedback between the two disturbances, which would promote the hypothesis that spruce beetles control stand dynamics during inter-fire periods.

Understory plant communities may also play an important role in linking fire and beetle interactions. The response of the understory plant community to spruce beetle disturbance may act independently, in conjunction, or in opposition to decreases in canopy sublimation to alter the properties of subsequent fires. Carter et al. (2022) observed increases in understory plant cover 10 years after a spruce beetle outbreak. The increase in cover may shade the soil and increase moisture retention that could have otherwise been evaporated via canopy opening. Shading provided by the understory canopy may work in conjunction with increases in snowpack to help retain snowpack for longer in the season, similar to the snow holding properties of *Artemisia tridentata* (Tedesche et al. 2017). Increases in snowpack and understory cover have both been observed a decade following spruce beetle outbreak and thus may have lasting implications for fuel moisture. Alternatively, significant increase in understory cover may decrease the substrate limitation of future fires by increasing fuel connectivity which may promote future fire spread, especially of low severity surface fires.

Because both spruce beetle outbreaks and fires typically occur in periods of drought, the ability of spruce beetle disturbance to mediate the effects of drought on surviving trees is potentially important. As spruce beetle outbreaks occur across the landscape, they reduce competition for resources and remove some of the largest competitors from the landscape. Forest vapor pressure deficits have been observed to decrease following spruce beetle outbreaks (Frank et al. 2019). If spruce beetles thin a stand, are the remaining trees less flammable due to more water per tree? There is evidence to suggest that the effects of drought as they relate to bark beetle outbreaks on stands can be minimized by thinning treatments (Restaino et al. 2019). Thus, investigating the water balance in stands and individual stems and how it may act as a mechanism for disturbance interactions is also an important topic of future research.

Climate change occurs as highly variable alterations to local environments: some areas are warming and drying while others are warming and receive more precipitation but in different forms than historic norms. Climatic changes in the subalpine will likely influence the occurrence of these two climatically dependent disturbances. However, the alteration of environmental conditions by one disturbance may influence conditions needed for stand regeneration post disturbance. Research conducted by Carlson et al. (2021) observed changes in the microclimate after spruce beetle outbreaks, specifically decreases in average minimum temperature. These changes in the subcanopy temperature have only been observed on the microclimate scale and have not been quantified across landscapes. Decreases in the subcanopy temperatures may help offset warming trends that favor future disturbances. Importantly, we have not discussed the thresholds by which the predominant driver of interaction transitions from being environmental condition mediated to substrate mediated. These thresholds will be important to identify as well as the ways in which one disturbance may bring us closer or farther away from the threshold.

Complimentary methods

One further avenue for research is explicit investigation of how processes operating at various temporal scales influence disturbance interactions. These processes are likely to operate on different time scales based on specific mechanism and the order of disturbances. Within the literature surveyed, Hart et al. (2014) observed that when the first disturbance is a fire, the reduction in substrate (i.e., host trees needed for spruce beetle outbreak) reduces the ability for spruce beetle outbreaks to occur prior to forest regeneration to size classes preferred by spruce beetles as habitat. The time needed for forest regeneration may itself vary based on the growth rates (as determined by temperature, precipitation, light availability, nutrient availability, etc.) of host trees. Additionally, the importance of substrate mediating mechanisms may also vary as a function of time and stand structure. Page et al. (2014) observed changes to litter flammability that were temporally explicit after spruce beetle outbreak. Leaf chemistry was altered because of spruce beetle outbreak across the canopy. These changes in flammability only lasted until host trees dropped their needles. The importance of substrate as a mechanism influencing successive fires may be more important over short timescales and stand characteristics (i.e., structure). Similarly, the importance of environmental mediating mechanisms for controlling a second disturbance may also vary based on temporally explicit processes such as stand development, although this remains unknown.

In addition, given the slow nature of forest development and dynamics that play out over centuries to millennia, potential mechanisms may vary not only within stand development but through long-term trends in climate and environment. Current investigations incorporate some aspects of temporal variation; 40% of papers (10 of 25) depend on or use dendrochronological methods to investigate the interactions of these two disturbances. However, these records—while beneficial to our understanding—are limited in scope, often on the scale of decades to potentially centuries. Palaeoecological records can incorporate multidecadal to millennial-scale trends and contextualize modern patterns accordingly. Incorporating palaeoecological perspectives into neo-ecological studies can enable a deeper understanding of disturbance timing, mechanisms and future regime shifts by providing a long-term context to ecological trends (Wingard et al. 2017; Buma et al. 2019).

Although fires are frequently reconstructed via palaeoecological methods, the use of pollen records or beetle remains to reconstruct spruce beetle outbreaks is less common (Morris et al. 2015). Under ideal conditions, it may be possible to reconstruct disturbance regimes beyond fire to incorporate spruce beetle outbreaks as well (Morris et al. 2015). When possible, combining fire and beetle palaeoecological records with neo-ecological observations to produce long-term estimates of beetle outbreaks could shape our understanding of not only the timing of disturbances in the subalpine, but also the resilience of these systems.

Challenges to generalizability

One major limitation to developing a framework to understand fire–beetle interactions is spatial: A large spatial bias exists within the published literature (Fig. 1) with 76% of the research (19 of 25) occurring in Colorado. Including studies conducted in Utah, 88% of literature (22 of 25) on fire and spruce beetle interactions emerge from the Southern Rocky Mountains. Two articles (8%) used within the literature review were from the Kenai peninsula of AK (Fig. 1c, d) and only 1 article (4%) was from Canada, potentially due to disturbance extent. These studies have been important for developing hypotheses for the interactions; however, it is important to link these findings to various geographic areas to promote generality which is an important yet difficult goal of disturbance ecology as a field (Jentsch and White 2019; Buma 2021). The Northern Rocky Mountains and Cascade Range represent a large area that contain both disturbance agents, the same species, and similar climatic pressures, yet remain underrepresented within the literature. Investigating disturbances across this geographic region may elucidate trends that are not present in the Southern Rocky Mountains due to differences in natural histories, species compositions, or spatial differences in the external drivers of each disturbance. Additionally, because the subalpine zone occurs at lower elevations at more northerly latitudes, trends present in the Southern Rocky Mountains may not occur at higher elevations.

Conclusions

The relative importance of the mechanisms that control interactions between spruce beetle outbreaks and fire in high elevation spruce–fir forests remain unclear. There is a need to understand both the patterns and processes underlying these two highly critical disturbances in these systems. Environmental condition mediating mechanisms may be better suited for understanding the interactions between spruce beetles and fire in subalpine spruce–fir forests because similar climatic conditions control both. Both disturbances can alter environmental conditions through hydrologic and energy balances which are potentially important for the second disturbance. These alterations may be mediated through overstory and understory plant structure, but our understanding of the influences environmental condition mediating mechanisms have on disturbance interactions is limited and warrants future study. There has been relatively little research on the linked/compound disturbance system despite its importance and geographic range, though there are other fields that have investigated individual mechanisms. By explicitly focusing on the influences and effects of environmental mediating mechanisms on disturbance interactions and expanding the scope of research both spatially and temporally, we may identify additional patterns that increase the predictability of this disturbance interaction.

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Data availability The dataset generated during the current study are available in Table 1.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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