Bark beetle and defoliator interactions across Pacific Northwestern forests

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Abstract

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The dynamics of irruptive forest insects are changing rapidly in response to climate warming, altering many important ecosystem services and often overwhelming budgetary and logistical resources allocated to mitigate the ramifications of outbreaks. Changes in outbreak dynamics have been reported for many insects across the world; however, the patterns are not consistent among or within taxa. Increases in outbreak size, severity, and duration have been largely attributed to warming temperatures, increases in drought, and changes in forest structure and composition for bark beetles and defoliators. In my dissertation, I used historical aerial survey data (1960-2019) from the coniferous forests of Oregon, Washington, and British Columbia to quantify the spatial dynamics of bark beetles, defoliators, and their interactions across local and regional scales, and to measure how these dynamics have changed through time. I was able to identify common patterns of increasing spatial autocorrelation through time for insect species that inhabit higher latitudes and elevations, and identify that there is greater spatial overlap of bark beetle and defoliator outbreaks in more recent decades. I also investigated drivers of population dynamics in Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae: Scolytinae), which shows a greater propensity for outbreaks in the interior Douglas-fir *Pseudotsuga menziesii* (Mirbel) regions east Cascade Range than in the coastal Douglas-fir regions west of the Cascades. I evaluated how Douglas-fir beetle abundance in eastern and western Washington was influenced by a suite of weather, natural enemy, and forest metrics, finding that climate and Douglas-fir beetle outbreak proximity and size appear to best explain the differences in the abundance of Douglas-fir beetle populations in eastern and western Washington. Lastly, I investigated the role of invertebrate natural enemies and competitors in providing top-down pressure on low density Douglas-fir beetle populations in eastern and western Washington by mapping and quantifying interactions beneath the bark using ImageJ software, and identifying all emerged species. Findings suggest that the robust interspecific competitor community in the interior Douglas-fir forests did not appear to play a major role in limiting Douglas-fir beetle population densities and suggests competition does not likely play a role in western Washington. *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae) may play a key role in limiting endemic Douglas-fir beetle populations in coastal Douglas-fir forests as it prefers moister habitats, while predaceous Coleoptera may perform better in the drier interior forests, but be limited in their top-down pressure on Douglas-fir beetle populations as many are generalist predators. Understanding insect outbreak dynamics and their interactions over broad spatial and temporal scales, identifying the top-down and bottom-up factors influencing these changes, and quantifying how these patterns may change under a warming climate is vital to developing effective management plans for forest ecosystems.

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Dedication

For Mom, Dad, and Heather.

Chapter 1: The spatial and temporal patterns of bark beetle and defoliator outbreaks, and their interactions, across the Pacific Northwest

Abstract

The dynamics of irruptive forest insects are changing rapidly in response to climate warming; however, the patterns are not consistent among or within taxa. Changes in outbreak dynamics for individual species have received much recent attention, but the potential for interactions among species has received far less. With the evidence of climate-mediated shifts in insect outbreak dynamics in recent decades, it is inevitable that there will be changes in the interactions between and among species. I used historical aerial survey data (1960-2019) from the coniferous forests of Oregon, Washington, and British Columbia to quantify the spatial dynamics of bark beetles, defoliators, and their interactions across local and regional scales, and to measure how these dynamics have changed through time. I was able to identify common patterns of increasing spatial autocorrelation through time for insect species that inhabit higher latitudes and elevations (mountain pine beetle, spruce beetle, western balsam bark beetle, and two-year cycle budworm), and highlight that regional warming is likely the main driver of these landscape scale changes. Further, this work suggests that there is greater spatial overlap of bark beetle and defoliator outbreaks in more recent decades, particularly in historically colder ecosystems at higher elevations and latitudes; however, these patterns are also apparent in more temperate forests as is the case for the interaction between Douglas-fir beetle, western spruce budworm, and Douglas-fir tussock moth. Increases in overlapping disturbances have important implications for forest management, which could compromise forest resilience in vulnerable or sensitive ecosystems. Understanding how the spatial

and temporal patterns of individual and interacting forest insect outbreaks have changed is vital to identifying threatened ecosystems, developing effective management plans for these areas, and understanding how patterns may continue to change under a warming climate.

Introduction

The dynamics of irruptive forest insects are changing rapidly in response to climate warming, altering many important ecosystem services and often overwhelming budgetary and logistical resources allocated to mitigate the ramifications of outbreaks (Dale et al. 2001; Raffa et al. 2008; Weed et al. 2013; Pureswaran et al. 2018). Changes in outbreak dynamics have been reported for many insects across the world; however, the patterns are not consistent among or within taxa. For instance, Haynes et al. (2014) highlighted the complexity of climate change and insect outbreak dynamics by analyzing outbreak records of five pine-defoliating insects in Germany, finding that increased temperatures resulted in declines of outbreak cyclicity and severity for two species, increases in outbreak frequency for two species, and increases in outbreak occurrence for one species. Dendrochronological reconstructions of western spruce budworm *Choristoneura freemani* Razowski (Lepidoptera: Tortricidae) defoliation showed that outbreaks tended to be more regionally synchronous across western North America in the last century (Swetnam & Lynch 1993; Swetnam et al. 1995; Ellis & Flower 2017). However, similar reconstructions for mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae) outbreaks suggested that synchrony did not change at a regional scale over the past three centuries (Jarvis & Kulakowski 2015), even though outbreak severity did seem to be increasing (Bentz et al. 2010). These long-term studies highlight the complexity of insect outbreak dynamics, and the difficulty in generalizing the patterns across taxa.

Changes in outbreak dynamics for individual species have received much recent attention (Jepsen et al. 2008; Cudmore et al. 2010; Johnson et al. 2010; Tobin et al. 2014); however, the potential for interactions among species has received less attention. In one recent study, Ward & Aukema (2019) analyzed the influence of climate and interactions between an invasive defoliator, larch casebearer *Coleophora laricella* Hubner (Lepidoptera: Coleophora), and native bark beetle, eastern larch beetle *Dendroctonus simplex* LeConte (Coleoptera: Curculionidae), on a common host, tamarack

Larix laricina (Du Roi) Koch (Pinaceae). They reported that outbreaks of both species were best predicted by the proximity of conspecific outbreaks. They also noted that tree mortality from eastern larch beetle increased in areas that had been previously defoliated by larch casebearer, emphasizing the potential for one outbreaking species to facilitate an outbreak in another species. Similar interactions have been observed in Douglas-fir *Pseudotsuga menziesii* (Mirbel) Franco (Pinacea) forests in the southern Rocky Mountains where outbreaks by the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae) were observed to follow defoliation by Douglas-fir tussock moth *Orgyia pseudotsugata* McDunnough (Lepidoptera: Lymantriidae) and/or western spruce budworm (Wright et al. 1984; Fredricks & Jenkins 1988; Hadley & Veblen 1993; Cole et al. 2022). These prior studies generally focused on local to regional patterns as opposed to patterns across landscapes. Spatial and temporal overlap in the outbreak areas of multiple disturbance agents can have profound ecological and economic consequences, including undermining forest resilience and productivity (Millar & Stephenson 2015). Insect outbreaks in conifer-dominated forests are typically limited to specific host tree species or hosts within a genus (e.g., Douglas-fir beetle on Douglas-fir, mountain pine beetle on *Pinus* spp.), often resulting in positive growth responses (i.e., release from competition) for unaffected host species (Hadley & Veblen 1993; Hart et al. 2015). However, when multiple disturbance agents occur closely in time and space, compensatory responses may be slowed or eliminated altogether, resulting in potentially long-term changes to ecosystem function (Paine et al. 1998; Buma 2015).

Interacting biotic disturbance events are typically grouped into either linked or compound interactions based on how one influences the other and the resulting outcome (Buma 2015). Linked interactions are when one disturbance changes the likelihood and/or characteristics of the subsequent disturbance, while compound interactions are when the synergy of two or more disturbances affect the system in an unexpected or novel way (Hadley & Veblen 1993; Paine et al.

1998; Buma 2015). Spatial overlap of disturbance has been observed for many species, often resulting from correlated stochastic weather events over the landscape (i.e., the "Moran" effect; Moran 1953). However, research into patterns of spatial synchrony within and across feeding guilds is lacking (Liebhold et al. 2004; Raimondo et al. 2004). Linked and compound disturbances across many systems have been shown to yield "ecological surprises", eroding resilience and in some cases completely overwhelming it (Paine et al. 1998). With the evidence of climate-mediated shifts in insect outbreak dynamics in recent decades (Weed et al. 2013; Pureswaran et al. 2018; Simler-Williamson et al. 2019), it is inevitable that there will be changes in the interactions between and among species. Understanding how these interactions have played out over the past 60 years can offer insights into how they have changed and may continue to change under future climate regimes.

Forests of the Pacific Northwest region of North America are host to multiple insect disturbance agents whose outbreaks are monitored annually through aerial detection surveys. Aerial surveys of the forests in western United States and Canada began in the late 1940s, making them an extensive, long-term, publicly-available dataset that provides spatial and temporal data on insect herbivory to individual trees, stands and landscapes (Coleman et al. 2018; Westfall et al. 2019). These data provide an ideal opportunity to quantify potential interactions among disturbance agents and how they may have changed through time. Though manifold, the most ecologically and economically important native insect species in this region belong to two main feeding guilds: bark beetles (Coleoptera: Curculionidae: Scolytinae) and lepidopteran defoliators. Irruptive species of bark beetles kill trees by boring through the bark and consuming the phloem (Howe et al. 2022b) while defoliators consume the leaves or needles of trees, resulting in tree growth loss, reduced regeneration, and tree mortality in severe and sustained defoliation events (Nealis 2016). Within the Pacific Northwest region of North America, there are several bark beetle species and defoliators that attack species in Pinaceae commonly detected in aerial surveys (Table 1); thus, they could potentially interact across the region. The irruptive bark beetles of the region can be categorized into pulse driven species (e.g., Douglas-fir beetle, fir engraver *Scolytus ventralis* LeConte, and western pine beetle *Dendroctonus brevicomis* LeConte, western balsam bark beetle *Dryocetes confusus* Swaine) that rely on and respond to pulses in resources (i.e., damaged or weakened host trees; Aukema et al. 2016), and threshold limited species (e.g., mountain pine beetle, spruce beetle *Dendroctonus rufipennis* (Kirby)) that can undergo self-driving population growth once cross-scale thresholds are exceeded (Raffa et al. 2008; Howe et al. 2022b). Regional warming trends appear to be influencing species in both groups with populations at higher latitudes and elevations (e.g., mountain pine beetle, spruce beetle, western balsam bark beetle) showing the greatest increases in recent decades (Berg et al. 2006; Safranyik & Carroll 2006; Raffa et al. 2008; Aukema et al. 2016; Howe et al. 2022a). It is often assumed that bark beetles tend to exploit previously defoliated trees due to their reduced defensive capacity (Wallin & Raffa 2001); however, patterns of cross-correlation (i.e., how one disturbance correlates to a different disturbance) of insect outbreaks over extensive spatial and temporal scales are generally unknown. Moreover, quantification of the potential for cross-correlation among irruptive forest insects is critical to understanding the role of disturbance in forest ecosystems, and perhaps for sustainable forest management in an era of global change.

An overarching objective of this chapter is to identify how the spatial and temporal patterns of bark beetles, defoliators, and their interactions, have potentially changed across the Pacific Northwest between 1960 and 2018-2019. Among insect species in Pacific Northwestern forests, there is considerable variation in the year-to-year occurrence of outbreaking species, and in the amount of area affected. In some species, such as mountain pine beetle and western balsam bark beetle, the area affected has increased in recent decades while in others, the affected area has seemingly decreased or remained static (Figure 1). In this chapter, I used data from annual aerial detection surveys from Oregon, Washington, and British Columbia (British Columbia Ministry of

Forests & Canadian Forest Service 2019; USDA Forest Service 2019) between 1960 and 2019 to analyze the spatial and temporal interactions within and among bark beetles and defoliators. I also examined these patterns in focal species that are known to interact on common or co-occurring hosts throughout the region. Specifically, I quantified annual spatial autocorrelation for individual species of bark beetles, defoliators, and within the two groups (bark beetles or defoliators) to identify yearly and decadal shifts, and quantified spatial cross-correlation through time to ascertain if certain species or groups are facilitating or inhibiting outbreaks of other species or groups (i.e., linked interactions). I hypothesize that: 1) spatial autocorrelation has increased over time (1960 to 2018) for mountain pine beetle, western balsam bark beetle, spruce beetle, and bark beetles as a group as these species are temperature and/or threshold limited, but not necessarily for Douglas-fir beetle, fir engraver, and western pine beetle as these species are not temperature limited and tend to be pulse driven (Raffa et al. 2008; Aukema et al. 2016; Howe et al. 2022a); 2) spatial autocorrelation over time has remained stable for defoliators (individual species and as a group) and is not generalizable across individual species as all species included in analyses are known to have cyclical outbreak dynamics, suggesting that they do not respond to increasing tree stress or pulses in resources like some bark beetles; and 3) outbreaks by defoliators and bark beetles are spatially cross-correlated through time only when defoliators are the initial disturbance agent and act to predispose trees to bark beetle infestations by weakening tree defenses.

Materials and Methods

Study Area

The Pacific Northwest, here defined as Oregon, Washington, and British Columbia, is characterized by topographically variable landscapes with some of the most iconic and productive forests in the world (Franklin & Dyrness 1988; Watson et al. 2015). In this region, coniferous forests are a dominant landcover type, consisting primarily of trees from the Pinaceae family, ranging from the dense mesic *Tsuga heterophylla* zone to the open dry *Pinus ponderosa* zone (Franklin & Dyrness 1988). This study encompasses forests composed primarily of coniferous tree species and the irruptive insect species that cause disturbance to them in the Pacific Northwest (Table 1).

Data Acquisition

Insect disturbance data were compiled from annual aerial surveys, which consisted of polygon shapefiles across Oregon and Washington (USDA Forest Service 2019; www.fs.usda.gov/detail/r6/forest-grasslandhealth/insects-diseases/?cid=stelprd3791643) and British Columbia (British Columbia Ministry of Forests & Canadian Forest Service 2019; www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial_Overview/) for each year from 1960 to 2019. Data are available for each year as polygon shape files with each polygon containing information on disturbance agent, host tree species (for some disturbance agents), and the number of dead trees per unit area or severity level associated with damaging agent (minimum of 5 damaged trees per polygon). I also compiled data on the spatial distribution of tree species from range maps in North America (Little 1971), and used data from tree inventory tables in the United States (USDA Forest Service; (FIA)) and British Columbia (British Columbia Ministry of Forests; (VRI)) to evaluate the accuracy of the tree species range maps (Appendix A) and ensure only forested polygons were considered in analyses.

Data Processing

A grid consisting of a network of 10×10 km cells was overlaid onto the region using the *sf* package in Rstudio (Pebesma 2018; R Core Team 2022) to create spatially unique cells. The 100km^2 grid cell size was used to optimize computation time. I extracted the area (km^2) of primary host tree species based upon Little (1971) to determine all forested polygons suitable for potential insect disturbance. Primary host species distributions were compared to Forest Inventory Analysis (USDA Forest Service) and Vegetation Resources Inventory (British Columbia Ministry of Forests) to ensure accurate representation of host tree presence and absence within grid cells (Appendix A). All grid cells that did not contain primary host tree species were removed from the analyses. All islands >10km (e.g., Vancouver Island, BC) away from the coastline were excluded from spatial analyses as they lacked neighboring grid cells.

The finalized grid was then overlaid onto historical aerial survey data, which maps and characterizes biotic and abiotic disturbance in forest ecosystems (British Columbia Ministry of Forests & Canadian Forest Service 2019; USDA Forest Service 2019). The area (km^2) of disturbance recorded for each insect species from Table 1 was extracted from each cell by each year, resulting in an annual disturbance area total ranging from 0–100 km^2 for each grid cell and unique insect species. Annual disturbance area totals were standardized by the amount of available host(s) within each grid cell, resulting in an annual proportion of host tree(s) distribution affected. Some insect species are capable of affecting host trees over a large area due to widely distributed hosts (e.g., mountain pine beetle on lodgepole pine, *Pinus contorta* Douglas), while other species affect hosts that have more limited spatial distributions (e.g., western pine beetle on ponderosa pine, *Pinus ponderosa* Douglas ex. C. Lawson). Thus, an annual proportion of host tree affected for each disturbance agent allowed for a more standardized comparison (Figure 1). The year of disturbance was lagged by one year for all bark beetle species as there is roughly one year between when a tree is colonized and when the discolored foliage associated with its decline and mortality becomes visible from aerial surveys, resulting in one less year of data for bark beetles.

Spatial and Temporal Analyses

I used spline.correlog from the *ncf* package in Rstudio to quantify the spatial autocorrelation as well as the temporal cross-correlation of bark beetles and defoliators (Bjørnstad et al. 1999; Bjornstad 2020; R Core Team 2022). The *ncf* package was used because it allows for a nonparametric estimate of the spatial autocorrelation function, without assuming *a priori* a specific functional relationship, and can be used in bimodally-distributed data, which was common due to the high frequency of 0 (i.e., no recorded disturbance) among cells (Bjørnstad et al. 1999). This package also allows for the estimation of confidence intervals using a bootstrapping function, which allows for a statistical test of the estimates for the local spatial autocorrelation (the estimate between values in space as the distance between sampling locations approaches 0) and the spatial range (the distance over which spatial autocorrelation exists). I estimated spatial autocorrelation for each feeding guild (bark beetles and defoliators) and species for each year. I also estimated the spatial autocorrelation within a 10-year moving window, with a 5-year overlap (i.e., 1960-1969, 1965-1974…, 2000-2019), to determine if average decadal autocorrelation changed through time. Because the autocorrelation function for many species tended to hover above zero over large spatial ranges, I selected an autocorrelation value of 0.25 (where most autocorrelation estimates began to asymptote) for use in comparing estimates of the spatial range through time. The 95% confidence intervals were estimated based on 250 bootstrapped replications using the spline.correlog function in *ncf*. Least squares linear regression was fit to the estimates of the annual local autocorrelation and spatial range to quantify and test for statistical changes through time for individual species and feeding guilds (defoliators and bark beetles). This technique allowed for a simple but effective approach to highlight trends in spatial patterns through time. Due to many years of little or no recorded disturbance in western spruce budworm and two-year cycle budworm *Choristoneura biennis* Freeman (Lepidoptera: Tortricidae) between 1960-1970, lines were also fit to estimates of the annual local autocorrelation and spatial range based on values from 1970-2019.

I also quantified the spatial cross-correlation using *ncf* to measure how the occurrence of one disturbance agent spatially correlates to another disturbance agent within the same grid cell, which I estimated through time. In this case, I used the estimate of the local cross-correlation, and considered time lags for each year from 1 to 10 years (i.e. 1 year lag, 2 year lag, …, 10 year lag) within and among feeding guilds. I also considered specific insects that interact on common or co-occurring host trees; in this case, I used data from Douglas-fir beetle, Douglas-fir tussock moth, and western spruce budworm (all of which feed on Douglas-fir), and western balsam bark beetle, spruce beetle, and two-year-cycle budworm (as all potentially interact within forests comprising Engelmann spruce, *Picea engelmannii* Parry ex Engelm. (Pinacea), hybrid spruce, *P. engelmannii* × *glauca*, and subalpine fir *Abies lasiocarpa* (Hooker) Nuttall (Pinacea)). Least squares linear regression was fit to cross-correlation estimates (grouped by time between disturbances) to identify trends through time. I used a 10-year maximum time lag as preliminary results showed little correlation between grid cells beyond this point. The use of a temporally lagged cross-correlation analysis provided insights into whether outbreaks of one species are facilitating, impeding, or have no effect on outbreaks of other species.

Results

Between 1960 and 2018/2019, tree mortality attributed to bark beetles has been observed over 1.45 million hectares and 449,335 hectares of tree damage have been attributed to defoliators. Mountain pine beetle and western balsam bark beetle were the largest contributors among bark beetles, and western spruce budworm was the largest contributor among defoliators (Figure 1; Table 1). Standardizing tree mortality by host tree(s) distribution highlighted that while mountain pine beetle was still the largest contributor to these damage totals, western balsam bark beetle affected a similar proportion of its hosts' distribution (Figure 1B & 1F). Spruce beetle also appeared to be damaging a higher proportion of its host tree distribution in the past decade (Figure 1B & 1F).

Between 1960 and 2018/2019, outbreaks by bark beetles tended to be spatially autocorrelated over a greater spatial range relative to defoliators (Fig. 2A, D). Moreover, the local spatial autocorrelation of bark beetle outbreaks significantly increased through time ($\beta = 0.004$, $t(57) = 5.33$, $p < 0.05$, Fig. 2B; Fig. 3A), as did the spatial range ($\beta = 2.45$, $t(57) = 6.29$, $p < 0.05$; Fig. 2C; Fig. 3B), which increased dramatically beginning in 2000 and especially between 2000 and 2010 (Fig. 2C). The spatial autocorrelation of outbreaks by defoliators also increased significantly through time (Fig. 2D) including with regard to estimates of local spatial autocorrelation ($\beta = 0.004$, $t(58) = 3.34$, $p < 0.05$; Fig. 2E; Fig. 3C) and spatial range ($\beta = 0.50$, $t(58) = 2.10$, $p < 0.05$; Fig. 2F; Fig. 3D). Further analysis at the species level suggested that mountain pine beetle outbreaks from ~2000-2014 were largely responsible for the increase in the local autocorrelation and spatial range within the bark beetle feeding guild, while western spruce budworm outbreaks from ~1980-1993 and ~2000-2014 were largely responsible for the generally cyclical patterns observed for defoliators. When mountain pine beetle was excluded from the bark beetle group, the slope estimates of the local autocorrelation and spatial range still significantly increased through time ($\beta = 0.004$, $t(57) = 5.00$, $p < 0.05$; $\beta = 1.24$, $t(57) = 5.74$, $p < 0.05$, respectively; Fig. 3A, B). In contrast, when western spruce budworm was excluded from the defoliator group, the slope estimates of the local autocorrelation and spatial range were not significantly different from zero when assessed through time ($\beta = 0.003$, $t(58) = 1.80$, $p = 0.08$; $\beta = 0.30$, $t(58) = 1.50$, $p = 0.14$, respectively).

When considering individual bark beetle species, the slope estimates of local autocorrelation (Fig. 3A) and spatial range (Fig. 3B) of outbreaks significantly increased through time for mountain pine beetle, spruce beetle, and western balsam bark beetle (Table 2). The slope estimates of the local autocorrelation and spatial range of outbreaks were not significantly different from zero for

Douglas-fir beetle and western pine beetle (Table 2). Lastly, the slope estimate of the local autocorrelation of fir engraver outbreaks was not significantly different from zero while the slope estimate of the spatial range of outbreaks was (Table 2; Fig. 3B).

Among individual defoliator species, the slope estimates of the local autocorrelation values over time statistically increased from 1960-2019 for western spruce budworm and two-year cycle budworm (Table 2; Fig. 3C). Similarly, the slope estimates of the spatial range (Fig. 3D) values over time statistically increased from 1960-2019 for western spruce budworm ($\beta = 0.75$, $t(58) = 3.00$, $p < 0.05$) and two-year cycle budworm ($\beta = 0.92$, $t(58) = 4.11$, $p < 0.05$) (Table 2; Fig. 3D). When considering the local autocorrelation and spatial range values through time from 1970-2019, statistically increasing slope estimates were observed for two-year cycle budworm, but not western spruce budworm (Table 2; Fig. 3C, D). Lastly, the slope estimates of the local autocorrelation and spatial range values were not significantly different from zero for western blackheaded budworm *Acleris gloverana* (Walsingham) (Lepidoptera: Tortricidae, western hemlock looper *Lambdina fiscellaria lugubrosa* (Hulst) (Lepidoptera: Geometridae, and Douglas-fir tussock moth through time (Table 2).

Considering the spatial cross correlation of outbreaks through time, from 1960-2018, bark beetle outbreaks were spatially cross correlated regardless of time between disturbances. However, slope estimates of the spatial cross correlation statistically decreased when disturbances were 5-10 years apart (Fig. 4A). In contrast, slope estimates of the spatial cross correlation of defoliator outbreaks increased statistically from 1960-2019, regardless of time between disturbances (Fig. 4B). Low spatial cross correlation was observed across all years when looking at relationships between bark beetle and defoliator outbreaks, regardless of initial disturbance agent (Fig. 4C, D). Specifically, slope estimates from 1960-2018/19 increased statistically when bark beetle outbreaks occurred 1-3 years before a subsequent defoliator outbreak (Fig. 4C), while statistical increases occurred 1, 2, and 10 years between outbreaks when defoliators were the initial disturbance agent (Fig. 4D).

Focusing on the spatial cross correlation of insect species that potentially interact on the same host tree resulted in similar patterns. Douglas-fir beetle outbreaks were spatially cross-correlated at shorter disturbance intervals (1-4 years between disturbances); however, no statistical changes were observed from 1960-2018, regardless of time between disturbances (Fig. 5A). The spatial cross correlation of western spruce budworm and Douglas-fir tussock moth outbreaks statistically increased from 1960-2019 and outbreaks were cross correlated for up to 9 years following initial disturbance (Fig. 5B). Low spatial cross correlation was observed across all years and disturbance intervals when Douglas-fir beetle was the initial disturbance agent; however, the slope estimates statistically increased from 1960-2018 for outbreaks that occurred 1-6 years apart (Fig. 5C). When western spruce budworm or Douglas-fir tussock moth were the initial disturbance agent, statistically increasing slope estimates were observed from 1960-2018 for outbreaks that occurred 1-10 years apart (Fig. 5D).

The spatial cross correlation of spruce beetle and western balsam bark beetle outbreaks statistically increased from 1960-2018, regardless of time between disturbances (Fig. 6A). Contrarily, the spatial cross correlation of two year cycle budworm only statistically increased when outbreaks were 4 years apart from 1960-2019 (Fig. 6B). Low spatial cross correlation was observed across all years and disturbance intervals when spruce beetle or western balsam bark beetle were the initial disturbance agent; however, statistical increases were observed from 1960-2018 for all disturbance intervals (Fig. 6C). Two-year cycle budworm outbreaks followed by spruce beetle or western balsam bark beetle outbreaks had low spatial cross correlation across all years and disturbance intervals; however, statistical increases occurred from 1960-2018 when outbreaks were 4-10 years apart (Fig. 6D).

Discussion

Understanding the spatial and temporal patterns of disturbance agents remains a frontier in ecology. The factors influencing outbreak patterns are diverse and often threshold driven, making it difficult to draw broad conclusions beyond individual species (Raffa et al. 2008; Bentz et al. 2010; Haynes et al. 2014; Pureswaran et al. 2018). In this chapter, I was able to identify common themes among feeding guilds and groups of disturbance agents, and highlight species and groups that do not follow any discernible patterns. Overall, bark beetles appear to be responding most strongly to changing conditions over the past 60 years as increases in host tree(s) mortality were observed for some species in the guild. These increases in tree mortality are mostly attributed to mountain pine beetle, western balsam bark beetle, and spruce beetle, all of which are likely benefiting from warming temperatures as they are historically limited by cold temperatures at higher latitudes and elevations (Bentz et al. 2010; Weed et al. 2015; Howe et al. 2022a). Pulse driven bark beetle species that inhabit lower elevations and latitudes, including Douglas-fir beetle, fir engraver, and western pine beetle, showed no change through time and appear unaffected by changing conditions during the past 60 years. Similarly, the impacts of all defoliators except two-year cycle budworm appear to be stable or decreasing in response to changing conditions over the past 60 years. Two-year cycle budworm inhabits higher latitudes and elevations, and thus may be benefiting from warming temperatures in these historically colder environments through reduced overwintering mortality similar to that suggested for western spruce budworm within the northern portion of its distributional range (Régnière & Nealis 2019). It is important to note that there is a paucity of research on two-year cycle budworm, so its response to warming temperatures remains largely unknown.

Measuring the spatial autocorrelation of outbreaks through time offers insights into how outbreak size and contiguity across the landscape have potentially changed. Bark beetles show the greatest increases through time, particularly over the last two decades. Increases in both the local autocorrelation and spatial range of bark beetle outbreaks from ~1995-2015 suggest that outbreaks have become larger and more contiguous across the landscape, though this increase was largely driven by mountain pine beetle outbreaks (Meddens et al. 2012). Statistically increasing trends over the past 60 years in the local autocorrelation and spatial range of mountain pine beetle, western balsam bark beetle, and spruce beetle outbreaks lends support for the conclusion that regional warming may synchronize outbreaks across the landscape (i.e., the "Moran" effect; Moran 1953). On the other hand, defoliators generally show static or decreasing spatial autocorrelation through time except for two-year cycle budworm. Two-year cycle budworm, as the name implies, is the only defoliator in this analysis that requires two years to complete development and inhabits subalpine forests similar to western balsam bark beetle and spruce beetle, indicating that regional warming trends are likely driving the observed increases in local autocorrelation and spatial range of outbreaks. The defoliators included in this study all exhibit cyclical population dynamics (Furniss & Carolin 1977; Wickman et al. 1981; Alfaro et al. 2014; Nealis 2016; Johns et al. 2016) that are largely thought to be driven by complex top-down and bottom up factors and thus may be limited in their ability to respond to regional changes (Royama 1984; Nealis 2016). Also, looking strictly at spatial autocorrelation of outbreaks may not be the best metric to measure changes through time for defoliators; rather, changes in outbreak cycle, severity, and duration, among others, may offer insights into how defoliators are responding to environmental changes (Haynes et al. 2014). For instance, the lack of observable shifts for western spruce budworm may be due to northward range expansion coinciding with range retractions along its southern distributional boundary, which could negate landscape level changes in the spatial correlation of outbreaks through time (Tai & Carroll 2022).

The spatial overlap of insect outbreaks through time at a landscape scale highlights the variability of interactions and the potential for one outbreak to influence another. Historical legacies of fire suppression coupled with more recent warming temperatures have resulted in a surplus of susceptible trees across the landscape (Hessburg et al. 2005; Taylor et al. 2006; Franklin & Johnson 2012), which can differentially influence bark beetle and defoliator populations. Taylor et al (2006) showed that fire suppression led to over 3 times the amount of susceptible pine for mountain pine beetle at the start of the current outbreak as compared to 100 years ago, emphasizing the influence of anthropogenic factors beyond climate change on insect outbreaks. The negative spatial cross-correlation of grouped bark beetle outbreaks through time is likely being driven by the recent extensive mountain pine beetle outbreak, and could be a result of rapid resource depletion as all susceptible trees are colonized and killed, requiring dispersal to unaffected areas (Safranyik & Carroll 2006). The lack of spatial cross correlation of Douglas-fir beetle outbreaks through time is likely a result of the relatively smaller, patchier outbreak dynamics following pulses of susceptible trees from stochastic disturbance events (e.g., windthrow, slash from harvesting) (Aukema et al. 2016) instead of regional phenomena (e.g., climate change). Moreover, though regional warming may be increasing underlying tree drought stress, these trends do not necessarily increase pulses of resources, thereby limiting the ability of pulse driven bark beetles to respond to changing climatic conditions, particularly for species inhabiting lower elevations and latitudes towards their southern distributional ranges. In contrast, statistical increases in the spatial cross-correlation of spruce beetle and western balsam bark beetle outbreaks through time, regardless of the time between disturbances, are likely due to warming conditions directly improving beetle fitness (Negron & Popp 2009; Bentz et al. 2010) and/or indirectly reducing host tree defensive capacity (Harvey et al. 2021; Howe et al. 2022a), lending further support for regional warming trends that promote more sustained and potentially overlapping outbreaks.

The increasing positive spatial cross-correlation of defoliator outbreaks across all decades and disturbance intervals is likely driven solely by western spruce budworm based on the similar patterns observed with it and the overall guild (Figs. 4b and 5b), suggesting that changing conditions may be promoting more sustained and chronic defoliation patterns in recent decades (Maclauchlan et al. 2006, 2018), but not necessarily larger or more severe outbreaks (Fig. 1C). Statistically increasing positive spatial cross-correlation when outbreaks are 4 years apart suggests this also may be the case for two-year cycle budworm. These changes through time could be a result of advanced tree regeneration following decades of fire suppression, creating dense multistoried forests that promote sustained defoliation events and improve successful dispersal through the canopy, particularly for western spruce budworm (Maclauchlan & Brooks 2009; Flower et al. 2014). Increases in the duration of defoliator outbreaks has important implications for subsequent bark beetle outbreaks as past research has highlighted the role of defoliation in predisposing trees to bark beetle attacks by reducing host tree defensive capabilities (Wright et al. 1984; Fredricks & Jenkins 1988; Hadley & Veblen 1993; Cole et al. 2022).

When focusing on insect species and groups of insect species known to interact on common or co-occurring host tree species, it was noteworthy that while the spatial cross-correlation of outbreaks was low across all groupings, there were, in fact, interactions at a landscape scale and changes over the past 60 years. Statistical increases in the spatial cross-correlation through time for bark beetle and defoliator outbreaks that occur closely together in time could be an artifact of increased disturbance by individual species within a limited spatial extent, making disturbance overlap among species inevitable. This is evident in the observed shift from historically negative to currently positive spatial cross-correlation 1-6 years between disturbance when bark beetles were the initial disturbance agent in the interaction with Douglas-fir beetle, Douglas-fir tussock moth, and western spruce budworm. Douglas-fir beetle preferentially attacks stressed and weakened trees that likely lack the nutritional quality needed to support spatially widespread defoliation, suggesting that the phenomenon of bark beetle outbreaks predisposing defoliator outbreaks is doubtful.

Furthermore, similar patterns were observed across all disturbance intervals for western balsam bark beetle, spruce beetle, and two-year cycle budworm, suggesting that regional warming is promoting disturbance overlap across the entire range of this study, which lends further support for the inevitable overlap as outbreaks increase. Regardless of the mechanism, spatial and temporal overlap in biotic disturbance events poses challenges to ecosystem resilience and to the capacity of land managers to respond (Buma 2015; Millar & Stephenson 2015; Seidl et al. 2017; Agne et al. 2018). When Douglas-fir tussock moth and western spruce budworm were the initial disturbance agent, statistical increases in the spatial cross-correlation through time across all disturbance intervals were evident, suggesting that defoliator outbreaks may be acting to predispose forests to subsequent Douglas-fir beetle outbreaks at a landscape scale. Similarly, when two-year cycle budworm was the initial disturbance agent, statistical increases (negative in 1960 to positive 1980-2018) in the spatial cross-correlation when disturbance were 4-10 years apart indicates the same may be true for western balsam bark beetle and spruce beetle, which lends more support for the propensity of greater spatial overlap as outbreaks increase across the landscape.

Through the lens of a warming climate, the expectations of how disturbances in confer-dominated forests will change is complex. This research has highlighted that bark beetles show the greatest propensity for change, and this change is likely due to regional warming. Greater drought stress as a consequence of this warming will likely promote greater bark beetle caused tree mortality as tree defensive capacity is compromised. However, increasing drought stress may also reduce the nutritional content of the overall tree during chronic or severe drought events, potentially limiting population growth. Further, high intensity fire is also projected to continue increasing as it gets warmer and drier across the region, which could limit insect outbreaks in general as potentially suitable and susceptible trees are removed from the system. Greater overlapping bark beetle activity, drought stress, and high intensity fire will all likely constrain the potential for defoliator outbreaks as these disturbances reduce the availability and nutritional quality of suitable host material.

Understanding how the spatial and temporal patterns of individual and interacting forest insect outbreaks have changed is vital to identifying threatened ecosystems, developing effective management plans for these areas, and understanding how patterns may continue to change under a warming climate. I was able to identify common patterns of increasing spatial autocorrelation through time for insect species that inhabit higher latitudes and elevations, and highlight that regional warming is likely the main driver of these landscape scale changes. Further, this work suggests that there is greater spatial overlap of bark beetle and defoliator outbreaks in more recent decades. These increases in the spatial overlap of outbreaks are most notable in historically colder ecosystems at higher elevations and latitudes, but these patterns are also apparent in more temperate forests as is the case for the interaction between Douglas-fir beetle, western spruce budworm, and Douglas-fir tussock moth. These increases in overlapping disturbances have important implications for forest management and may signal that forest resilience is eroding in these areas, though further research is required. Further work investigating how the changing climate and forest characteristics have potentially influenced the occurrence of overlapping disturbance in these areas would greatly improve our ability to potentially mitigate impacts. Identifying where forest resilience may be eroding is the first step in evaluating the potential for effective management plans.

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Tables

Table 1. Defoliators and bark beetles selected for analysis based on aerial detection surveys (Available from the British Columbia Ministry of Forests & Canadian Forest Service 2019; USDA Forest Service 2019; 1960-2019).

	Disturbance Agent	Primary Host(s)	Total Area affected, km^2		
			1960-1979	1980-1999	2000-2019*
Defoliators	Douglas-fir tussock moth *Orgyia pseudotsugata* McDunnough	Douglas-fir, True fir spp.	5348.8	1172.5	1102.0
	Two-year cycle budworm *Choristoneura biennis* Freeman	Engelman Spruce, Subalpine fir	43188.3	29242.8	27290.9
	Western blackheaded budworm *Acleris gloverana* Walsinham	Western hemlock, Mountain hemlock, True fir spp.	9298.2	3734.4	981.0
	Western hemlock looper *Lambdina fiscellaria lugubrosa* (Hulst)	Western hemlock, Douglas-fir, Mountain hemlock	1233.1	4881.2	1603.2
	Western spruce budworm *Choristoneura freemani* Razowski	Douglas-fir	31018.8	199267.0	89973.0
Bark beetles	Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins	Douglas-fir	8626.6	7460.0	14215.5
	Fir engraver *Scolytus ventralis* LeConte	True fir spp.	10031.4	18016.6	18228.9
	Mountain pine beetle *Dendroctonus ponderosae* Hopkins	Pine spp.	72951.3	94077.2	768553.0
	Spruce beetle *Dendroctonus rufipennis* Kirby	Engelman spruce, Sitka spruce, White spruce	6245.3	8545.5	32176.4
	Western balsam bark beetle *Dryocoetes confusus* Swaine	Subalpine fir, True fir spp.	1216.6	37600.7	332353.5
	Western pine beetle *Dendroctonus brevicomis* LeConte	Ponderosa pine	12540.6	5201.6	4380.0

Table 2. Least squares linear regression outputs of the local autocorrelation (distance lag = 0) and spatial range (where spatial autocorrelation decreases below 0.25) of outbreaks for bark beetles and defoliators through time. Statistically increasing regression lines are displayed in Figure 3.

	Local Autocorrelation				Spatial Range			
Disturbance Agent(s)	Intercept (± SE)	Slope (± SE)	t stat.	Adj. R^2	Intercept (± SE)	Slope (± SE)	t stat.	Adj. R^2
All Defoliators	-8.086 (±2.64)	0.004** (±0.001)	3.34	0.147	-939.1 (±474.1)	0.50* (±0.24)	2.10	0.055
All Defoliator Excluding western spruce budworm	-5.715 (±3.51)	0.003 (±0.002)	1.80	0.037	-561.8 (±397.6)	0.30 (±0.20)	1.50	0.021
Douglas-fir tussock moth	-2.778 (±3.91)	0.002 (±0.002)	0.77	-0.007	-122.2 (±177.5)	0.07 (±0.09)	0.73	-0.008
Two-year cycle budworm	-20.093 (±5.08)	0.010*** (±0.003)	4.07	0.241	-1796.6 (±445.4)	0.92*** (±0.22)	4.11	0.245
Western blackheaded budworm	4.687 (±4.70)	-0.002 (±0.002)	-0.94	-0.002	418.6 (±238.9)	-0.21 (±0.12)	-1.71	0.032
Western hemlock looper	-4.320 (±3.52)	0.002 (±0.002)	1.29	0.011	-48.4 (±209.5)	0.03 (±0.11)	0.27	-0.016
Western spruce budworm	-17.485 (±3.95)	0.009*** (±0.002)	4.61	0.256	-1448.7 (±503.3)	0.75** (±0.25)	2.98	0.118
Two-year cycle budworm 1970 - 2019	-20.754 (±4.33)	0.011*** (±0.002)	4.91	0.282	-1375.9 (±413.5)	0.71** (±0.21)	3.40	0.152
Western spruce budworm 1970 - 2019	1.719 (±2.85)	0.0004 (±0.001)	-0.30	-0.019	115.6 (±634.0)	-0.03 (±0.32)	-0.09	-0.021
All Bark Beetles	-6.413 (±1.35)	0.004*** (±0.001)	5.33	0.321	-4771.6 (±775.6)	2.45*** (±0.39)	6.29	0.399

All Bark Beetles Excluding mountain pine beetle	-6.846 (±1.50)	0.004*** (±0.001)	4.99	0.292	-2406.7 (±429.5)	1.24*** (±0.22)	5.74	0.356
Douglas-fir beetle	1.621 (±2.22)	-0.001 (±0.001)	-0.47	-0.014	-117.9 (±248.0)	0.07 (±0.13)	0.60	-0.011
Fir engraver	-3.417 (±2.76)	0.002 (±0.001)	1.39	0.016	-553.0 (±257.3)	0.29* (±0.13)	2.23	0.064
Mountain pine beetle	-4.204 (±1.95)	0.002* (±0.001)	2.55	0.086	-3655.8 (±878.2)	1.88*** (±0.44)	4.26	0.228
Spruce beetle	-10.980 (±3.03)	0.006*** (±0.002)	3.79	0.187	-607.7 (±253.3)	0.32* (±0.13)	2.48	0.082
Western balsam bark beetle	-26.307 (±2.35)	0.013*** (±0.001)	11.39	0.690	-4313.5 (±403.1)	2.19*** (±0.20)	10.80	0.666
Western pine beetle	-3.787 (±2.41)	0.002 (±0.001)	1.78	0.036	104.9 (±280.1)	-0.04 (±0.)14	-0.28	-0.016

* Denotes statistical significance at $\alpha = 0.05$

** Denotes statistical significance at $\alpha = 0.01$

*** Denotes statistical significance at $\alpha = 0.001$

Figures

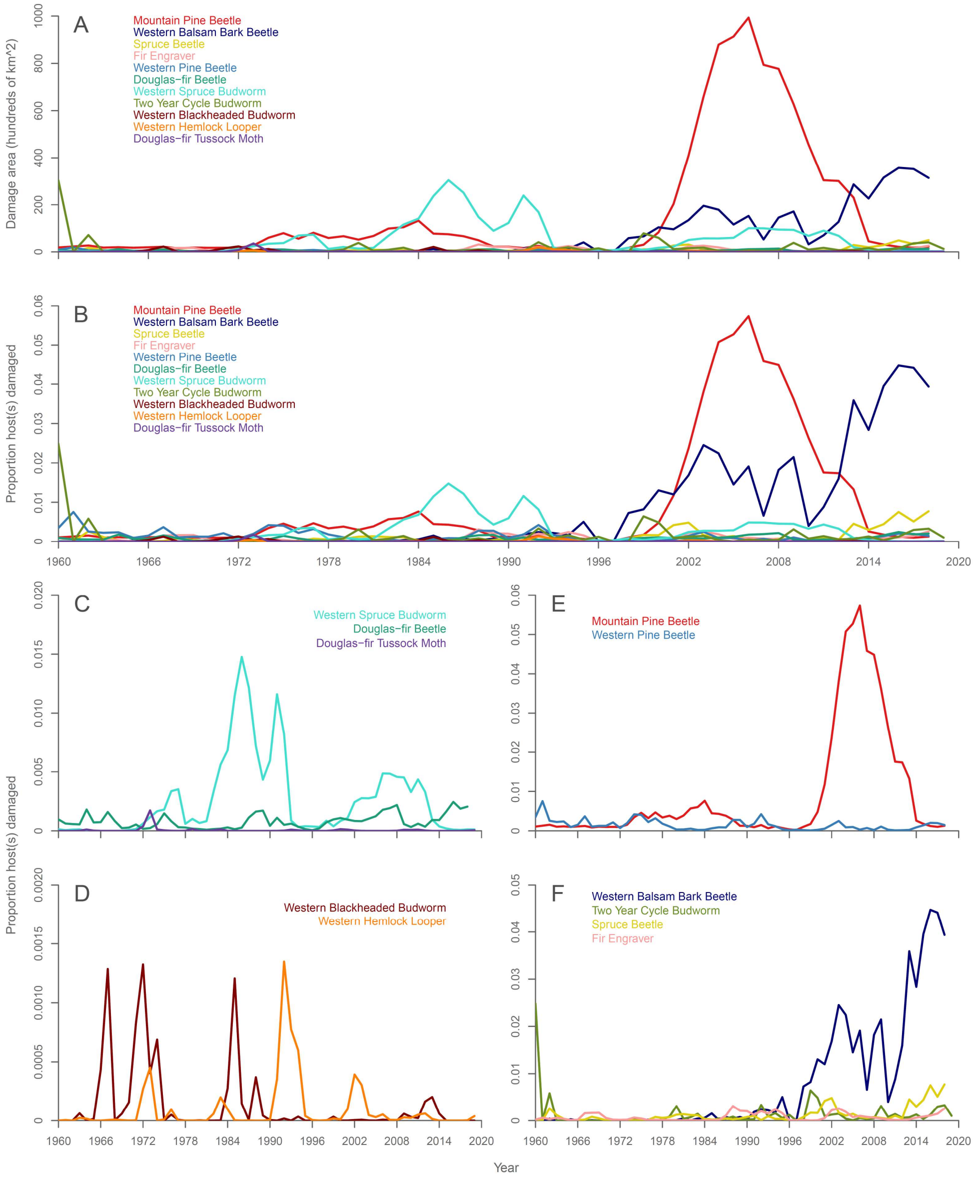


Figure 1. Annual forest area recording outbreaks (A) and proportion of host trees damaged (B) for the species listed in Table 1 from 1960-2019. Insect species have been separated by common host tree species or genus in figures C-F; proportion of *P. menziesii* damaged (C), proportion of *Tsuga spp.* damaged (D), proportion of *Pinus spp.* mortality (E), and proportion of *Abies spp.* and *Picea spp.* damaged (F). Proportion of host(s) affected (y-axis) was calculated by dividing the area disturbed (Aerial suverys from the British Columbia Ministry of Forests & Canadian Forest Service 2019; USDA Forest Service 2019) by the area of available primary host(s) tree species (Little 1971) for panels B-F. Some insect species are capable of millions of hectares of tree damage due to widely distributed hosts (e.g. mountain pine beetle on lodgepole pine), while others have more limited host distributions (e.g. western pine beetle on ponderosa pine); thus, an annual proportion of host tree affected for each disturbance agent allows for a more standardized comparison.

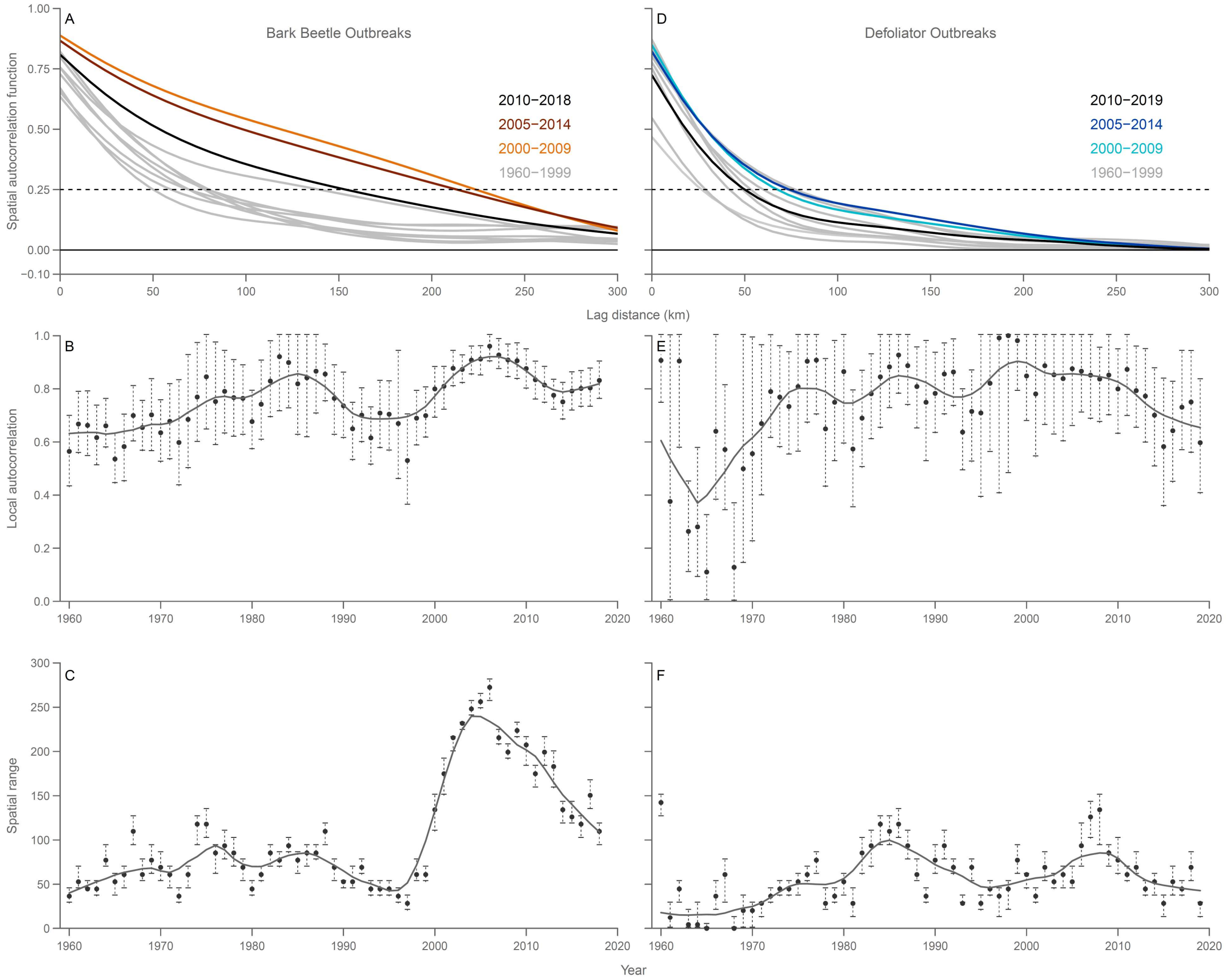


Figure 2. The spatial patterns of bark beetle and defoliator outbreaks through time. Spline correlograms estimating the spatial autocorrelation of outbreaks aggregated by overlapping decades (i.e. 1960-1969, 1965-1974…, 2000-2019) for bark beetles (A) and defoliators (D). Colored lines highlight the increased local and regional spatial autocorrelation of bark beetle outbreaks in recent decades (orange lines), but no changes for defoliator outbreaks (blue lines). Annual local autocorrelation (distance lag = 0) for bark beetles (B) and defoliators (E) from 1960- 2019 (2018 for bark beetles) with loess trend line. Annual spatial range where autocorrelation decreases below 0.25 for bark beetles (C) and defoliators (F) from 1960- 2019 (2018 for bark beetles) with a loess trend line.

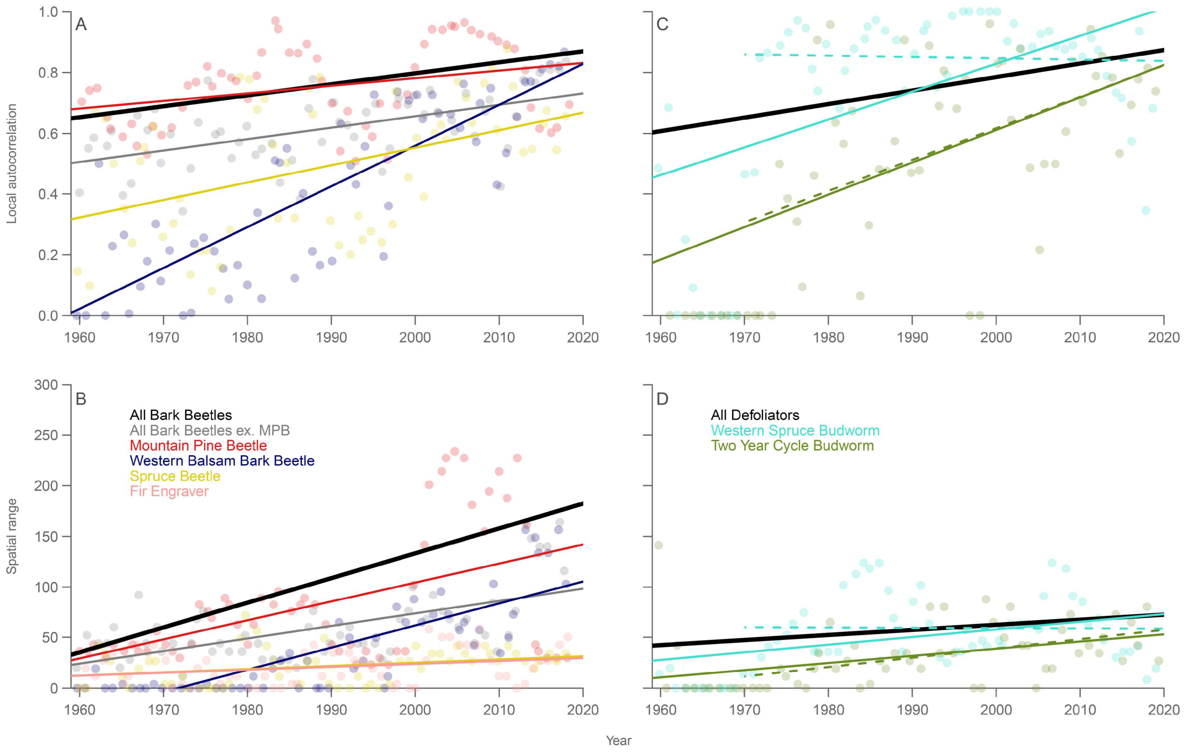


Figure 3. Least squares linear regression lines of the local autocorrelation (distance lag = 0) and spatial range (where autocorrelation decreases below 0.25) of outbreaks for bark beetles and defoliators through time. Only significant (p-value <0.05) regression lines are shown (refer to Table 2 for regression output values). Dashed lines in panels C and D are trend lines from 1970-2019 displaying the change to a negative trend for western spruce budworm depending on the initial year; the same trend was observed for two-year cycle budworm regardless of initial year.

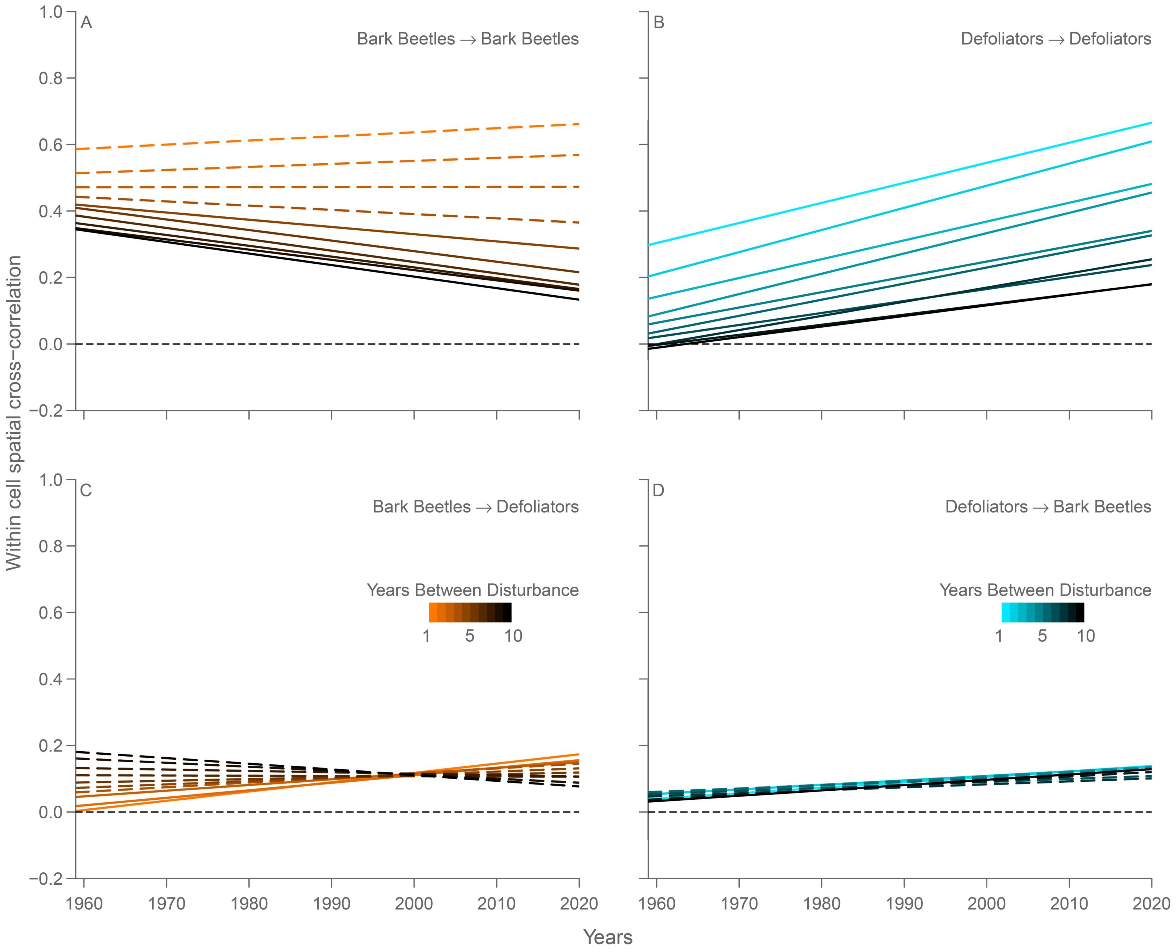


Figure 4. The local spatial (within 10 x 10 km) cross-correlation of bark beetle and defoliator outbreaks from 1960-2019 (2018 for bark beetles). Lines represent least squares linear regression fit to estimates of spatial cross correlation (grouped by years between disturbances) to identify trends through time. For example, the line representing a one-year time lag between disturbances (lightest colored lines) corresponds to all possible 1-year combinations from 1960-2019 (e.g. 1960-61, 1961-1962, 1962-1963…2018-2019). Similarly, the line representing a two-year time lag between disturbances is corresponds to all possible 2-year combinations from 1960-2019 (e.g. 1960-1962, 1961-1963… 2017-2019), and so on for each time lag to 10 years between disturbances (black lines). Solid lines represent slope estimates that were statistically different from zero and dashed lines represent slope estimates that were not statistically different from zero. Correlograms measure the cross-correlation (how a variable relates to a different variable) as distance (lag) increases. Within cell spatial cross-correlation corresponds to the y intercept (lag = 0) of the spline correlogram. Outbreak data was obtained from aerially detected survey data (British Columbia Ministry of Forests & Canadian Forest Service 2019; USDA Forest Service 2019; 1960-2019).

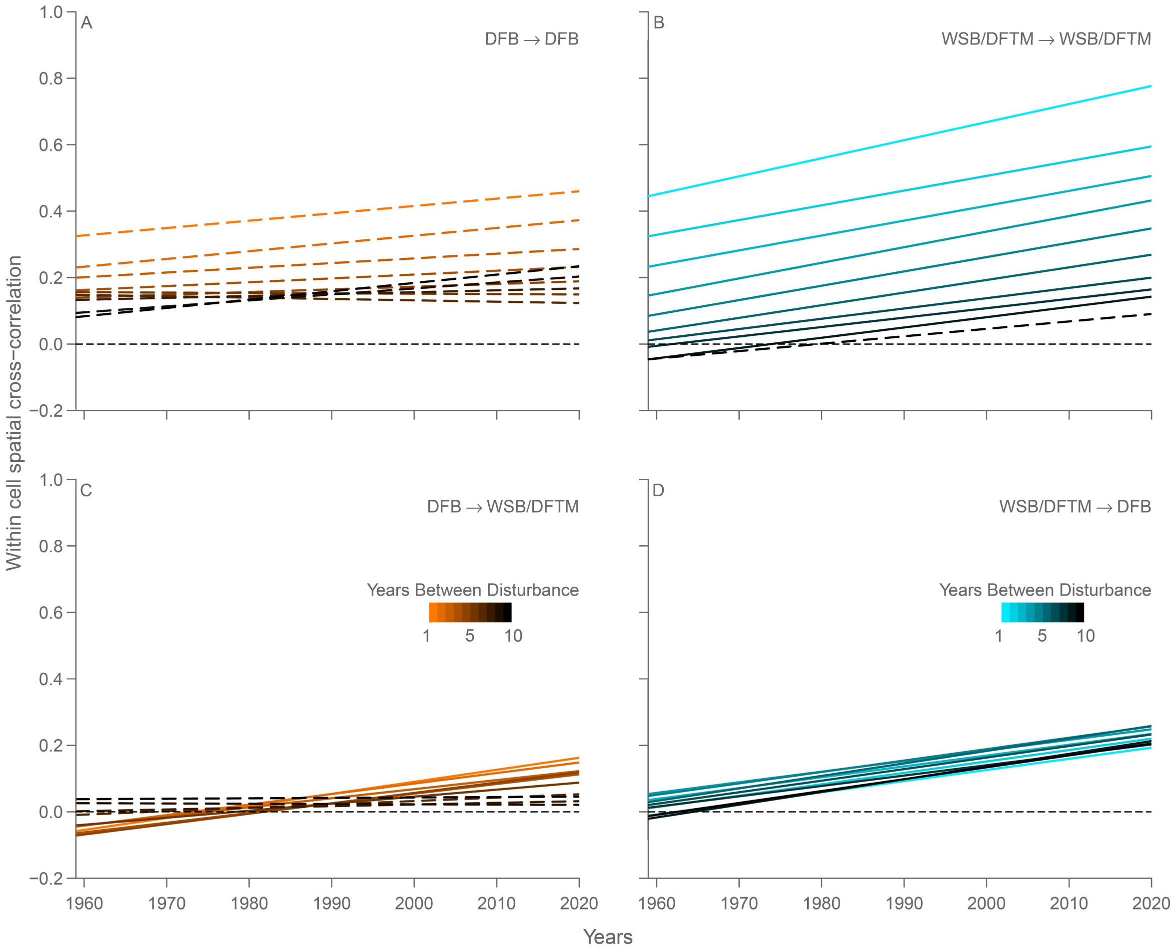


Figure 5. The local spatial (within 10 x 10 km) cross-correlation of Douglas-fir beetle (DFB) and western spruce budworm and Douglas-fir tussock moth outbreaks from 1960-2019 (2018 for DFB). Lines represent least squares linear regression fit to estimates of spatial cross correlation (grouped by years between disturbances) to identify trends through time. For example, the line representing a one-year time lag between disturbances (lightest colored lines) corresponds to all possible 1-year combinations from 1960-2019 (e.g. 1960-61, 1961-1962, 1962-1963…2018-2019). Similarly, the line representing a two-year time lag between disturbances is corresponds to all possible 2-year combinations from 1960-2019 (e.g. 1960-1962, 1961-1963… 2017-2019), and so on for each time lag to 10 years between disturbances (black lines). Solid lines represent slope estimates that were statistically different from zero and dashed lines represent slope estimates that were not statistically different from zero. Correlograms measure the cross-correlation (how a variable relates to a different variable) as distance (lag) increases. Within cell spatial cross-correlation corresponds to the y intercept (lag = 0) of the spline correlogram. Outbreak data was obtained from aerially detected survey data (British Columbia Ministry of Forests & Canadian Forest Service 2019; USDA Forest Service 2019; 1960-2019).

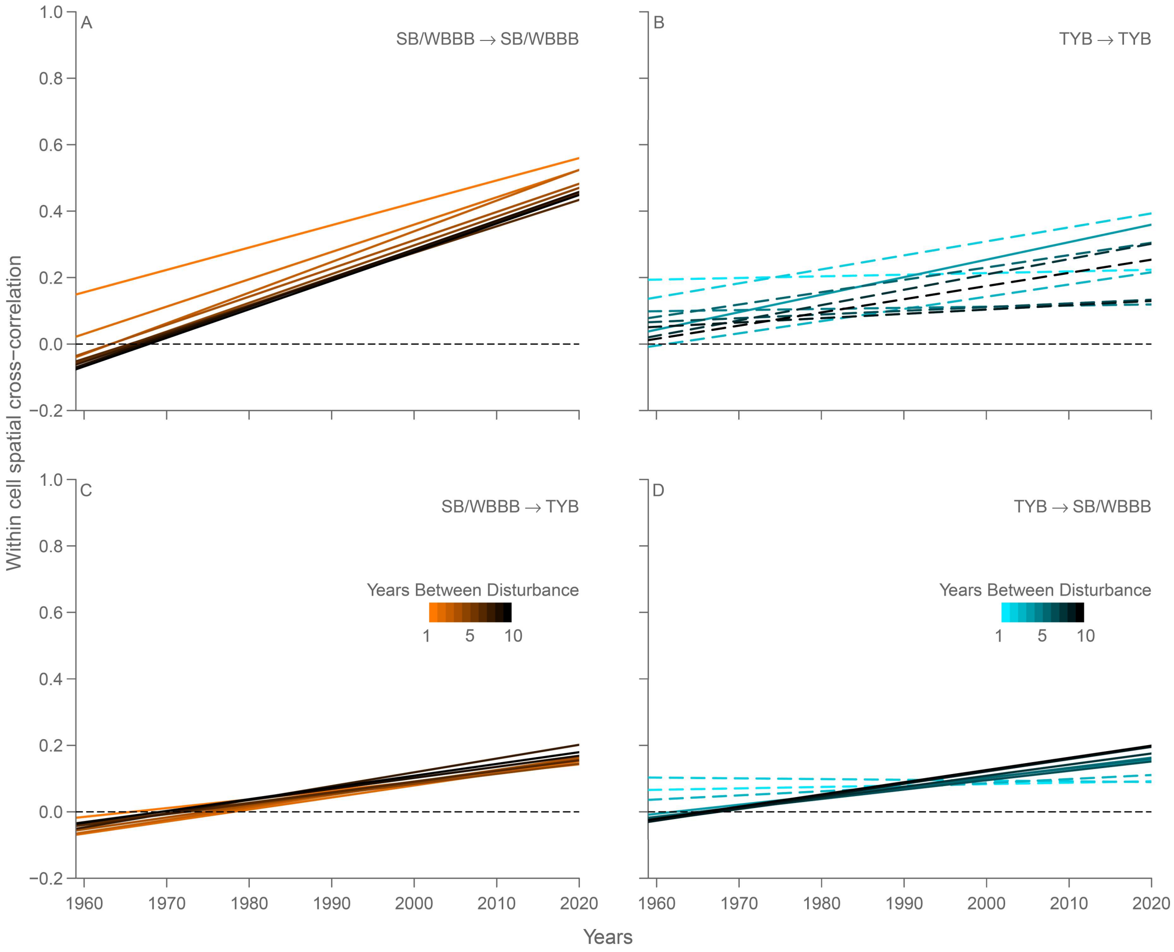
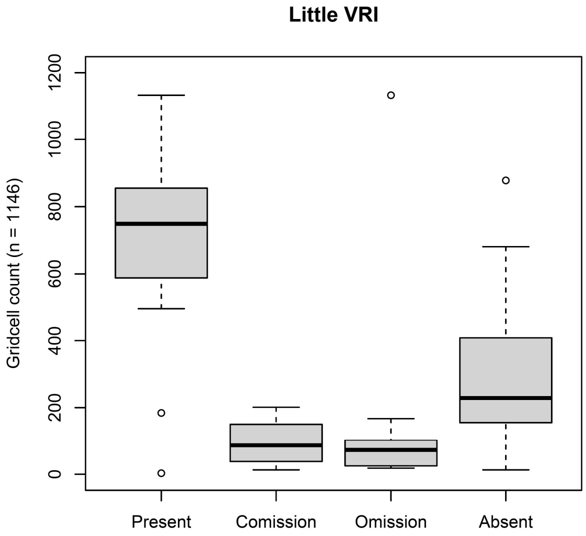


Figure 6. The local spatial (within 10 x 10 km) cross-correlation of spruce beetle and western balsam bark beetle, and two-year cycle budworm outbreaks from 1960-2019 (2018 for bark beetles). Lines represent least squares linear regression fit to estimates of spatial cross correlation (grouped by years between disturbances) to identify trends through time. For example, the line representing a one-year time lag between disturbances (lightest colored lines) corresponds to all possible 1-year combinations from 1960-2019 (e.g. 1960-61, 1961-1962, 1962-1963…2018-2019). Similarly, the line representing a two-year time lag between disturbances is corresponds to all possible 2-year combinations from 1960-2019 (e.g. 1960-1962, 1961-1963… 2017-2019), and so on for each time lag to 10 years between disturbances (black lines). Solid lines represent slope estimates that were statistically different from zero and dashed lines represent slope estimates that were not statistically different from zero. Correlograms measure the cross-correlation (how a variable relates to a different variable) as distance (lag) increases. Within cell spatial cross-correlation corresponds to the y intercept (lag = 0) of the spline correlogram. Outbreak data was obtained from aerially detected survey data (British Columbia Ministry of Forests & Canadian Forest Service 2019; USDA Forest Service 2019; 1960-2019

Appendix A



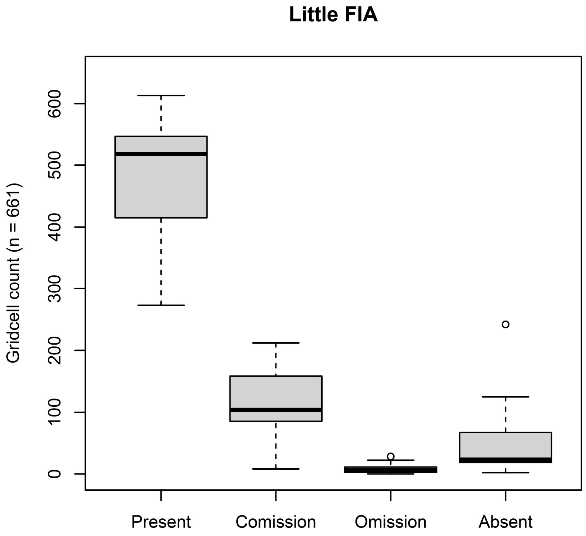


Figure A1. Comparison of the presence, absence, and error (comission and omission) of primary host tree (Table 1) range maps in North America (Little 1971) when compared to Forest Inventory Analysis (FIA; USDA Forest Service) and Vegetation Resources Inventory (VRI; British Columbia Ministry of Forests) to evaluate the accuracy of the tree species range maps and ensure only forested polygons were considered in analyses.

Chapter 2: The role of climate, weather, natural enemies, and forest stand characteristics in the population dynamics of Douglas-fir beetle and western spruce budworm

Abstract

Increases in the size, severity, and duration of bark beetle and defoliator outbreaks have been largely attributed to warming temperatures, increases in drought, and changes in forest structure and composition. Quantifying the responses of irruptive forest insects to climate, weather, natural enemies, and forest metrics is complex but necessary as the climate continues to change across the region. I investigated drivers of population dynamics in two species of particular interest in western North America; Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae: Scolytinae) and western spruce budworm, *Choristoneura freemani* Razowski (Lepidoptera: Tortricidae). Both species attack Douglas-fir *Pseudotsuga menziesii* (Mirbel) east and west of the Cascade Mountain Range; however, in recent decades outbreaks typically occur east of the Cascade Mountain Range. Trap capture data of adult western spruce budworm populations in coastal and interior Douglas-fir stands are presented in this chapter as a repository as COVID19 prevented further assessment of the population dynamics. Understanding how the factors that influence Douglas-fir beetle population dynamics differ between eastern and western Washington Douglas-fir forests is complex but necessary as the climate continues to change across the region. I evaluated how Douglas-fir beetle abundance (collected with multifunnel traps) in eastern and western Washington was influenced by a suite of predictor variables weather, natural enemies, and forest metrics. Overall, climate and Douglas-fir beetle outbreak proximity and size, appear to best explain the differences in

the abundance of Douglas-fir beetle populations in eastern and western Washington. Findings suggest that Douglas-fir beetle abundance in western Washington sites is limited more so by the smaller size of nearby conspecific outbreaks while the larger outbreaks serve to promote the generally higher population densities observed in eastern Washington sites. Furthermore, Douglas-fir beetle abundance increased with warmer minimum winter temperatures and higher summer climatic moisture deficits, but decreased with higher previous year maximum summer temperatures and previous year autumn climatic moisture deficits. Natural enemies appear to be numerically responding to the size of the Douglas-fir beetle population instead of providing top-down pressure. The abundance of Douglas-fir beetle increased with the proportion of Douglas-fir basal area in western sites, but does not appear to be an important factor in explaining the population differences between eastern and western sites. Understanding the factors that limit Douglas-fir beetle populations is vital in predicting how population dynamics may shift under changing climatic regimes.

Introduction

Substantial increases in outbreak size and severity have been observed for many forest insect species across the world. These changes have been linked to changes in climate because insect development and reproduction are regulated by temperature (Bale 1993; Bale et al. 2002). Several studies have shown that climate change has allowed some species to expand their geographical range and abundance (Battisti et al. 2005; Jepsen et al. 2008, 2011; Cudmore et al. 2010), whereas others have reported range retraction and decreased abundance (Johnson et al. 2010; Tobin et al. 2014a). For example, increases in winter temperatures can reduce insect overwintering mortality, leading to high population densities in the following spring and summer (Bale 1993; Weed et al. 2015). Increases in spring and summer temperatures can also directly affect forest insects, leading to earlier emergence in spring, accelerated developmental rates, and increased generations per year, all of which can exacerbate the extent of forest disturbance (Jepsen et al. 2011; Pureswaran et al. 2018). Warmer summer temperatures, especially in conjunction with summer drought, can increase host plant stress and consequently reduce host plant defensive responses to herbivory (Raffa et al. 2008). Lastly, warming temperatures could alter trophic interactions, especially when interacting species differentially respond to temperature (Tobin et al. 2014b; Uelmen et al. 2016; Furlong & Zalucki 2017).

Increases in outbreak size, severity, and duration have been largely attributed to warming temperatures, increases in drought, and changes in forest structure and composition for bark beetles (Mckee & Aukema 2015; Crocker et al. 2016; Seidl et al. 2016, 2017) and defoliators (Maclauchlan & Brooks 2009; Pureswaran et al. 2018; Simler-Williamson et al. 2019). The coniferous forests of western North America are host to several bark beetle and defoliator species, some of which cause widespread tree mortality with important ecological and economic consequences (Fig. 1). Two species of particular interest in the northwestern United States and southern British Columbia are

Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae: Scolytinae) and western spruce budworm, *Choristoneura freemani* Razowski (Lepidoptera: Tortricidae). Both of these native insect species can cause high levels of mortality in their primary host, Douglas-fir *Pseudotsuga menziesii* (Mirbel), with western spruce budworm typically consuming freshly flushed needles (Brooks et al. 1987) and Douglas-fir beetle boring through the bark and consuming phloem tissue (Furniss & Kegley 2014). Both species occur east and west of the Cascade Mountain Range (Fig. 2); however, in recent decades outbreaks have primarily occurred east of the Cascade Mountain Range, particularly for western spruce budworm (Brooks et al. 1987; USDA Forest Service 2019). For example, Douglas-fir beetle has caused ~1.36 million hectares (mha) of mortality in eastern Washington and Oregon but only ~0.62 mha in the west over the past 60 years (USDA Forest Service 2019). Even more contrasting is western spruce budworm, which has caused ~20.44 mha of tree damage in eastern Washington and Oregon, but only ~0.67 mha in western Washington and Oregon (USDA Forest Service 2019). As the climate continues to warm in these altered forests, it is unclear whether these patterns will continue, or if tree damage and mortality from these two insects will change (i.e., increase or decrease) in the western Cascade region.

Ecology and biology of Douglas-fir beetle

Douglas-fir beetle has a univoltine life cycle with a spring brood that overwinters as adults, and a summer brood that overwinters as larvae (Furniss 2014a; Aukema et al. 2016). In western Washington, spring brood adults generally emerge from under the bark in mid-April (Freeman et al. 2020) to seek a suitable host tree, whereby they release aggregation pheromones to attract mates and other females to mass attack the tree (Furniss & Kegley 2014). Once mated, females construct a vertical gallery in the phloem tissue of the tree where eggs are laid (Furniss 2014a; Furniss & Kegley 2014). Eggs hatch in 1-3 weeks and larvae begin feeding in horizontal galleries that terminate in pupal chambers, where pupation occurs in August-September (Furniss & Kegley 2014). Overwintering larvae typically emerge in July and generally attack trees that have been previously attacked by the spring brood; parent adults can also re-emerge in the summer to produce a second brood (Furniss & Kegley 2014).

Douglas-fir beetle is a relatively non-aggressive bark beetle that primarily attacks weakened and stressed Douglas-fir, but is capable of killing vigorous trees at high population densities (Negron 1998). This behavior results in patterns of relatively small, patchy mortality events in areas that have been previously disturbed or that show signs of reduced growth (Negron 1998; Six & Skov 2009). Though large-scale outbreaks are relatively uncommon in the Pacific Northwest, large and sustained (>3 years) outbreaks have been observed in the Rocky Mountains, often following widespread injury to trees by fire, drought, pathogens, and/or defoliation (Furniss et al. 1979; Hadley & Veblen 1993; Ryan & Amman 1996; Powers et al. 1999; Cole et al. 2022). Previous modeling efforts have been developed to predict the likelihood of Douglas-fir beetle infestations based upon bottom-up trophic constraints such as percent Douglas-fir in the stand, stand basal area, average stand age, average diameter at standard height, phloem thickness, bark thickness and tree growth rate over the previous 10 years (which is a proxy for tree stress); all show a positive relationship with the probability of infestation except for previous year tree growth rates, which shows a negative relationship (Shore et al. 1999; Negrón et al. 2001). Powers et al. (1999) investigated the influence of anomalous weather events and a state-level precipitation index on Douglas-fir beetle population growth rates, and reported that a lack of precipitation following a windthrow event increased the size of outbreaks from 1992-93 in the Willamette National Forest, Oregon. It is important to note that many of these models have been developed in interior Douglas-fir regions (e.g., Colorado Front Range) or the southwestern Cascade Range; thus, these relationships may differ in the coastal Douglas-fir region.

Ecology and biology of western spruce budworm

Western spruce budworm attacks and causes growth loss and occasional mortality in its primary host, *P. meziesii*, but can also cause damage and mortality in true firs (*Abies spp*. Mill.), particularly *Abies grandis* (Douglas ex D. Don) Lindley (Carolin & Coulter 1975; Brooks et al. 1987). It is univoltine across most of its range (Fellin & Dewey 1982). Adults emerge at the end of July and beginning of August, mate, and then females oviposit on the underside of needles (Dedes 2014). Eggs hatch in 7-10 days. First instars then disperse in search of crevices in the bark to spin hibernacula, molt into 2nd instars, and overwinter in diapause (Fellin & Dewey 1982; Dedes 2014). Western spruce budworm do not feed until the following spring, relying solely on energy reserves to disperse as neonates and overwinter. Warm temperatures (>20°C) during early diapause have been shown to decrease larval survival by increasing resource consumption and may be an important factor in limiting western spruce budworm outbreaks in the coastal Douglas-fir region (Nealis & Régnière 2016). Second instars emerge from hibernacula and disperse to branch tips in May, mining old needles and swelling buds until fresh foliage becomes available following budburst (Fellin & Dewey 1982). Synchrony between spring larval emergence and Douglas-fir budburst is critical for western spruce budworm fitness and may also be a key factor in limiting outbreaks in western Washington (Nealis 2012; Régnière & Nealis 2019; Tai & Carroll 2022). The larvae develop through a total of 6 instars before pupating in July; the pupal period lasts ~10 days (Fellin & Dewey 1982; Dedes 2014).

Most research on western spruce budworm has occurred in eastern Oregon, eastern Washington, and the southern interior of British Columbia (Brooks et al. 1987). At endemic levels, western spruce budworm populations typically cause only minor damage and are largely thought to be controlled by generalist predators (i.e., ants and birds; Brooks et al. 1987). Dominant, older, nonvigorous trees are often preferred by western spruce budworm larvae, which consume large amounts of biomass in the form of newly flushed foliage (Alfaro et al. 1982; Brooks et al. 1987; Maclauchlan & Brooks 2009). The preference of western spruce budworm larvae for large trees is adaptive as it provides a stable source of food with decreased risk of host mortality, while also facilitating larval dispersal down through the canopy onto unaffected subdominant trees when high population densities begin to deplete foliage (Brooks et al. 1987; Maclauchlan & Brooks 2009). Given this dispersal behavior, canopy structure has been shown to be an important stand susceptibility measure, with continuous, multistory canopies consistently supporting the highest levels of defoliation and mortality (Brooks et al. 1987; Maclauchlan & Brooks 2009). Other bottom up factors, such as stand density and stand composition, are important measures of stand susceptibility, with higher density stands composed of primarily host tree species being most susceptible to western spruce budworm defoliation (Brooks et al. 1987; Maclauchlan & Brooks 2009). At the site level, particularly in more northern latitudes, dry and warm conditions have been shown to increase western spruce budworm activity; for example, south facing aspects, mid elevations, steep slopes, and ridgetops have been linked to increased larval feeding (Brooks et al. 1987). Flower (2016) compiled multiple dendrochronological reconstructions over the past 300 years of outbreaks across western North America, highlighting that drought conditions consistently preceded western spruce budworm outbreaks, synchronizing regional outbreaks up to 2,000 km apart.

Climate and forest characteristics of the Pacific Northwest

The climate of the western cascade mountain range (hereafter referred to as the coastal Douglas-fir region) is typified by moist, mild winters and summer drought conditions (Franklin & Dyrness 1988). The forests of this region comprise the *Tsuga heterophylla* (Raf.) Sarg. and *Picea sitchensis* (Bong.) Carr. zones, aptly named for the dominant climax tree species, but are commonly dominated by Douglas-fir throughout most of the successional trajectory (Franklin & Dyrness 1988). The climate of the eastern Cascade Mountain Range (hereafter referred to as the interior Douglas-fir region) is characterized by cold, snowy winters, hot and very dry summers, and a shorter growing season (Franklin & Dyrness 1988). In addition to *P. menziesii,* the forests of this region are composed of *Pinus ponderosa* Douglas ex Lawson, *A. grandis*, *Pinus contorta* Douglas, and occasionally *T. heterophylla*, *Thuja plicata* Donn ex Don, and *Picea engelmanii* Perry ex Engelm. (Franklin & Dyrness 1988).

The climate across the Pacific Northwest has changed over the past century, with annual mean temperatures increasing 0.6-0.8°C from 1901-2012 (Abatzoglou et al. 2014). Increasing maximum and minimum temperatures have also been observed across all seasons, with the largest increases occurring during winter months, while decreasing summer and autumn precipitation have increased climatic water deficits across the region (Abatzoglou et al. 2014). Forest structure and composition have also changed over the past century in both the coastal and interior Douglas-fir regions. In the coastal Douglas-fir region, intensive management for timber harvesting has shifted forests from ~50% old-growth forests to >40% fragmented, single-age, monoculture *P. menziesii* stands <50 years old (Franklin & Johnson 2012; Agne et al. 2018). In the interior Douglas-fir region, selective logging of large dominant *P. ponderosa* and *P. menziesii* trees from the historically dry-open forests, and fire suppression, have resulted in increases in dense, multistoried, contiguous forests with a higher composition of *P. menziesii* (Hessburg et al. 1999, 2005). It remains unclear whether a warming climate and differential changes in forest stand characteristics will continue to promote or inhibit outbreaks of Douglas-fir beetle and western spruce budworm, and how these changes affect the natural enemy communities associated with Douglas-fir beetle and western spruce beetle.

Natural enemies of Douglas-fir beetle and western spruce budworm

Natural enemies, particularly invertebrate predators, have been shown to provide top-down control over endemic bark beetle populations, but have little effect on irruptive epidemic populations due to predator satiation (Moeck & Safranyik 1984; Reeve 1997). Moreover, increases in natural enemy densities typically lag host/prey populations in both time and space (Moeck & Safranyik 1984; Furniss & Kegley 2014). Most of the studies that identified natural enemies of Douglas-fir beetle were conducted ~60 years ago and often under disparate conditions and locations. For example, Cowan & Nagel (1965) studied an outbreaking Douglas-fir beetle population in the Siuslaw National Forest, while Marsden et al. (1981) estimated the top-down pressure of natural enemies in the intermountain west. Some studies have been completed in more coastal Douglas-fir forests, but typically concentrated in southwestern Oregon (Ryan & Rudinsky 1962; Kline & Rudinsky 1964) or in the Olympic Peninsula (Johnsey et al. 1965). It remains unclear whether the natural enemy communities associated with Douglas-fir beetle are equally represented in the disparate ecosystems of the coastal and interior Douglas-fir regions of Washington.

Among parasitoids that attack Douglas-fir beetle, most have been reported to be Hymenopteran species within Braconidae (which are generally larval parasitoids; e.g., *Coeloides vancouverensis* (Dalla Torre)) and Pteromalidae (which generally parasitize adults; e.g., *Karpinskiella paratomicobia* Hagen and Caltagirone). Predators of Douglas-fir beetle have also been well studied, and include species from Coleoptera (e.g., *Enoclerus sphegeus* (Fabricius)*, Thanasimus undatulus* (Say)*, Temnoscheila chlorodia* (Mannerheim)), Diptera (e.g., *Medetera spp., Lonchaea spp.*), and Raphidoptera (e.g. *Agulla spp.*), which collectively attack larval and adult stages of Douglas-fir beetle (Kline & Rudinsky 1964; Johnsey et al. 1965; Marsden et al. 1981; Moeck & Safranyik 1984; Zack et al. 1998; Furniss 2014b).

For western spruce budworm, various species of ants (Formicidae) have been shown to be important generalist predators, as ascertained through exclosure experiments, while other predaceous insects, including species within Raphidioptera, which also prey on Douglas-fir beetle, have received less attention (Carlson et al. 1984; Brooks et al. 1987). Parasitoids from Hymenoptera (Braconidae, Ichneumonidae, Trichogrammatidae, and Chalcidoidea) and Diptera (families Tachinidae and, to a lesser extent, Sarcophagidae) have been well studied in western spruce budworm populations, and collectively parasitize all immature stages (Carolin & Coulter 1959; Torgersen et al. 1984; Schaupp et al. 1991; Huber et al. 1996; O'Hara 2005; Bennett 2008; Fernandez-Triana & Huber 2010). Despite this prior attention on parasitoids and predators of western spruce budworm, no records seem to exist from endemic western spruce budworm populations in the coastal Douglas-fir region. It was my initial intention to document the natural enemy community and its role in endemic Douglas-fir beetle and western spruce budworm populations in sites west and east of the Cascade Mountain Range. Unfortunately, due to the COVID19 pandemic, the insectary that was the only reliable source of western spruce budworm for use in sentinel studies was not operational during the pandemic, and I was only able to acquire life stages for pilot studies in 2019. I was able to continue work on the natural enemies of Douglas-fir beetle despite the pandemic, and understanding their role on the population dynamics of the beetle remains an important avenue of research, especially as the climate and forest stand characteristics continue to change.

The overall objectives of this study were to assess the relative roles of bottom-up forest stand metrics (e.g., relative basal area, tree species diversity) and top-down trophic interactions with invertebrate natural enemies on endemic Douglas-fir beetle populations in coastal and interior Douglas-fir field sites in Washington, and assess the role of regional climatic trends in affecting host tree susceptibility to Douglas-fir beetle. The overarching goal was to quantify the role of these abiotic and biotic factors on the dynamics of Douglas-fir beetle in the eastern and western Cascade Mountain Range to better understand how changes might affect their future population dynamics.

Management practices have differentially altered the forest composition and structure across the region, potentially affecting host tree availability for Douglas-fir beetle (Hessburg et al. 1999, 2005; Franklin & Johnson 2012; Agne et al. 2018). I hypothesized that a lack of suitable host trees in the coastal Douglas-fir region from extensive clearcut harvesting restricts the development of Douglas-fir beetle outbreaks, while selective logging and fire suppression have resulted in an abundance of suitable host trees in the interior Douglas-fir region, promoting outbreaks. I also surmised that climate warming has increased water deficits across the region (Abatzoglou et al. 2014; Restaino et al. 2016), intensifying drought in the already drought prone interior Douglas-fir region, but not the moist coastal Douglas-fir region (Franklin & Dyrness 1988). Consequently, I hypothesized that a lack of susceptible host trees due to less intensive drought stress has limited Douglas-fir beetle outbreaks in the coastal Douglas-fir region, but intensive drought stress in the interior Douglas-fir region has resulted in an abundance of susceptible host trees. Because of the important role that natural enemies play in endemic populations of Douglas-fir beetle (Moeck & Safranyik 1984; Reeve 1997), I also hypothesized that natural enemy communities are more abundant and diverse in coastal Douglas-fir relative to interior Douglas-fir, providing increased top-down control on endemic Douglas-fir beetle populations in the former but not the later. Although I was not able to conduct a multi-year study on western spruce budworm natural enemies, I was still able to monitor adult populations in coastal and interior Douglas-fir stands, and present these data, without formal analyses, in this chapter as a repository.

Materials and Methods

Experimental Design

In 2019, I used U.S. Forest Service aerial detection survey data (USDA Forest Service 2019) to identify one site in western Washington and two sites in eastern Washington (Fig. 2). Additionally, one site (Cedar River) was added in western Washington in 2020 and two sites (Darrington and North Bend) were added in western Washington in 2021. Sites that were selected had no recorded Douglas-fir beetle outbreaks in the preceding five years, and comprised primarily Douglas-fir, defined as >50% basal area represented by Douglas-fir (Weatherby & Thier 1993; Freeman et al. 2020). At each site, I installed 3-6 circular plots (11.3 m radius) and deployed HOBO Pro V2 data loggers (Onset Computer Corporation, Bourne, Massachusetts) to record hourly temperatures. In each plot, I deployed one 12-unit multifunnel trap (Synergy Semiochemicals Corporation, Delta, British Columbia) baited with Douglas-fir beetle aggregation pheromones (frontalin and sudenol) and ethanol (Alpha Scents Inc., West Linn, Oregon) to quantify its densities and the invertebrate natural enemy community. Traps were deployed in April and removed in early September. Plots were separated by a minimum distance of 100 m along a transect. I also deployed one UNI-Trap (green; Alpha Scents Inc., West Linn, Oregon) baited with western spruce budworm sex pheromone (Z11-14Ac, E11-14OH, E11-14Ald and E11-14Ac; Alpha Scents Inc., West Linn, Oregon) in each plot to quantify western spruce budworm densities; UNI-Traps were deployed in Mid-July and removed in early September. I collected density data for Douglas-fir beetle and its invertebrate natural enemies, and western spruce budworm males, in 2019, 2020, and 2021. Natural enemies were identified to species in most cases using microscopy with reference keys and photographs from several sources (Ryan & Rudinsky 1962; Kline & Rudinsky 1964; Cowan & Nagel 1965; Johnsey et al. 1965; Marsden et al. 1981; Dahlsten 1982; Moeck & Safranyik 1984; Aspöck 1986; Bright 1987; Evans & Hogue 2006; Goheen & Willhite 2006; Furniss 2014b).

To quantify forest stand metrics, I identified and measured the diameter at standard height (DSH, ~1.4 m from the ground) of all stems >5 cm within each plot and within one randomly selected area adjacent each plot (~100m from plot center randomly in 8 possible cardinal and intercardinal directions). I used ArcGIS to measure the distance between sites and the nearest

Douglas-fir beetle outbreak from U.S. Forest Service aerial detection survey data (USDA Forest Service 2019). I used the GTOPO30 digital elevation model, which has a horizontal grid spacing of 30 arc seconds (approximately 1 km; U.S. Geological Survey 1996), to extract the elevation, aspect, and slope for each site. I also used the GTOPO30 digital elevation model (U.S. Geological Survey 1996), to calculate the mean elevation and the coefficient of variation of elevation (i.e., "hilliness") within a 10 x 10 km region centered on each site. I used ClimateNA (Wang et al. 2016) to extract climate and weather variables including the following: mean maximum temperature in winter (December (previous year) - February), spring (March - May), and previous year spring, summer (June – August), and autumn (September - November), mean minimum temperature in winter and spring, Hargreaves climatic moisture deficit in spring, summer, and previous year spring, summer, and autumn, and previous year annual heat moisture index. The suite of extrapolated site level weather values obtained from ClimateNA were used in lieu of the temperatures recorded from deployed HOBO Pro V2 data loggers due to missing data. Site level monthly mean temperature values from ClimateNA and from deployed HOBO Pro V2 data loggers were compared using least squares linear regression with a resulting adjusted $r^2 = 0.99$, suggesting that data from ClimateNA did reflect weather conditions at my sites. A complete list and description of all predictor variables is presented in Table 1. Collectively, these data were used to test the hypotheses that host tree availability and susceptibility is greater in eastern than western Washington which limits Douglas-fir beetle outbreaks in the west, but not the east.

Statistical Analysis

To test if host tree availability and susceptibility were greater in eastern than western Washington, I quantified the effect of forest metrics (e.g., tree species richness and diversity index, relative basal area of Douglas-fir), landscape metrics (e.g., coefficient of variation and mean of elevation, distance from Douglas-fir beetle outbreak in current and previous year, size of nearest Douglas-fir beetle outbreak in current and previous year), and weather metrics (e.g., mean minimum winter temperatures, mean maximum summer temperatures, climatic moisture deficits) on Douglas-fir beetle funnel trap abundance; a complete list of predictor variables can be found in Table 1. Due to the large number of explanatory variables, I used least absolute shrinkage and selection operator (LASSO; Tibshirani 1996) in the *glmnet* package (Friedman et al. 2022) in R (R Core Team 2022) to identify a subset of potentially important predictor variables from a larger set of predictor variables. This approach is similar to stepwise regression; however, variable selection and parameterization are improved when using LASSO, particularly when there are numerous explanatory variables and potential multicollinearity between variables (Tibshirani 1996; Hastie et al. 2009a). I determined a statistically important subset of predictor variables on the log10-transformed abundance of Douglas-fir beetle by performing 100 LASSO regressions and selecting variables that were present in the final model $\geq$ 80% of the time (adapted from Freeman et al. 2020). Because LASSO tends to bias coefficient estimates toward zero (Hastie et al. 2009b), all predictor variables in the subset with non-zero estimates were then analyzed using generalized linear mixed-effects models (GLMM) in the *lmerTest* package (Kuznetsova et al. 2022), allowing for the inclusion of interaction and random effects into the model. As multifunnel traps located along the same transect were likely to be spatially autocorrelated, a random effect of transect was included in the glmm models and evaluated with a log-likelihood ratio test using *ranova* in the *lmerTest* package (Kuznetsova et al. 2022).

Two generalized mixed effects models were developed to assess the role of forest, landscape, and weather metrics on the log10 abundance of Douglas-fir beetle, and to understand how these metrics differed in eastern and western Washington. The first model included all variables identified through LASSO with the addition of a random effect of transect. To explore if covariates differentially influence the log10 abundance of Douglas-fir beetle in eastern and western

Washington, I evaluated a second model containing everything in the first model with the inclusion of side (defined as east or west of the Cascade Range) as a fixed effect and two-way interaction term between all predictor variables. For both models, all main, random, and interaction effects (for the second model) were fit in a full model and backwards elimination was used to identify the best predictive model for each. Multicollinearity between fixed effects was first evaluated by calculating variance inflation factors (VIF) with the *car* package (Fox et al. 2019), resulting in the iterative removal of the variable with the highest value until all variables had a VIF < 10 (Montgomery et al. 2012). Next, the variable with the highest p-value was removed in each iteration until only variables with p-values < 0.05 remained. Inevitably, there was a high degree of multicollinearity between side and other predictor variables; however, the inclusion of the main and interaction effects with side did offer insights into how the influence of each variable potentially changes in eastern and western Washington. A least squares regression was fit to the predicted log10 Douglas-fir beetle abundance outputs for each model (with and without side), which resulted in an adjusted $r^2 = 0.96$, suggesting that the multicollinearity introduced by side did not negatively affect model performance (Fig. 3). Final models were compared using Akaike's information criterion (AIC).

Natural enemies were evaluated further using a two-sample Wilcoxon rank sum test to test the hypothesis that natural enemies were more abundant and diverse in western than eastern Washington, and thus serve to provide greater top-down pressure on western Douglas-fir beetle populations. The non-parametric test was used because the natural enemy data was not normally distributed and attempts to normalize the data through transformations were not successful, in part due to the extreme bimodal distribution in the natural enemy data. Because there were higher numbers of Douglas-fir beetle in eastern Washington, and natural enemies typically show a numerical response to prey (Moeck & Safranyik 1984; Reeve 1997), natural enemy abundance and diversity were standardized by the log10 abundance of Douglas-fir beetle per trap.

Results

Douglas-fir beetle and western spruce budworm were found at all sites and in all years in which traps were deployed (Figs. 4 & 5). Eastern sites had a higher average per trap catch of Douglas-fir beetle (4,582 vs 1,668 in western sites) and a higher average per trap catch of natural enemies (67 vs 5 in western sites). Overall, two predaceous beetles, *Thanasimus undatulus* (Say) (Coleoptera; Cleridae) and *Enoclerus sphegeus* (Fabricius) (Coleoptera: Cleridae), were the most abundant natural enemies with a combined total of 2,277 in eastern Washington and 195 individuals in western Washington. The predaceous beetles *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae) and *Temnoscheila chlorodia* (Mannerheim) (Coleoptera: Trogossitidae) were only captured in eastern sites (23 and 115, respectively). Similarly, 480 individuals identified from *Agulla* (Raphidioptera: Raphidiidae), for which species are possible predators of Douglas-fir beetle (Aspöck 1986; Zack et al. 1998), were collected in eastern sites, and only 1 individual was collected from a western site in North Bend, Washington. *Coeloides vancouverensis* (Dalla Torre) (Hymenoptera: Braconidae) was the most abundant parasitoid and only collected in eastern sites (19 individuals); however, it is important to note that the parasitoid community was not well represented in the multifunnel traps. Research suggests that *C. vancouverensis* utilizes visual and vibrational cues to locate Douglas-fir beetle larvae; thus, semiochemically baited multifunnel traps may not be an effective method to assess the parasitoid community (Ryan & Rudinsky 1962). The Wilcoxon tests of the standardized richness and diversity index of natural enemies in eastern and western Washington echoed the summary statistics above with eastern sites having statistically richer ($W = 242.5$, $p < 0.001$) and more diverse ($W = 604$, $p < 0.001$) natural enemy communities than western sites.

Relationships between the log10 Douglas-fir beetle abundance and the variables selected by LASSO analysis highlight that the pattern for many of these variables are the same in eastern and western Washington; however, values of variables from eastern sites are generally more extreme, particularly among the weather variables (Fig. 6). For instance, log10 Douglas-fir beetle abundance increases with current year winter minimum temperature across all sites, but it is generally much colder in eastern sites (Fig. 6G). Similarly, log10 Douglas-fir beetle abundance decreases when the previous year autumn Hargreaves climatic moisture deficit is high for all sites, but there are 3 times greater deficits in eastern sites (Fig. 5J). The LASSO analysis revealed that many of these variables were important predictors of log10 abundance of Douglas-fir beetle (Table 2). After accounting for multicollinearity and backwards elimination of nonsignificant variables, the final model excluding side contained proportion of Douglas-fir basal area, proximity to nearest Douglas-fir beetle outbreak in the previous-year, size of nearest current-year Douglas-fir beetle outbreak, current-year mean minimum winter temperature, current-year summer Hargreaves climatic moisture deficit, previous-year maximum mean summer temperature, and natural enemy species richness (Table 2). Based on the model output, the log10 abundance of Douglas-fir beetle increased with proportion of Douglas-fir basal area, size of nearest current-year Douglas-fir beetle outbreak, current-year mean minimum winter temperature, current-year summer Hargreaves climatic moisture deficit, and natural enemy species richness, but decreased with proximity to nearest previous-year Douglas-fir beetle outbreaks and previous-year maximum summer temperature (Table 2; Fig. 6).

Similar results were observed in the second model containing the main and two-way interaction terms of side (east or west) and the random effect of transect (Table 2). Most of the interaction terms were not significant predictors of the log10 abundance of Douglas-fir beetle, and/or had extreme VIF values (>2000); only the interaction between side and proportion of Douglas-fir basal area was included, along with the main effect of side. Inclusion of side as a main effect highlighted that the log10 abundance of Douglas-fir beetle is significantly less in western sites. The interaction term also showed that there was no effect of proportion of Douglas-fir basal area on the log10 abundance of Douglas-fir beetle in eastern sites, but a significant positive relationship in western Washington sites (Table 2; Fig. 6E). Sites from western Washington had a higher mean proportion of Douglas-fir basal area (0.65 vs 0.45 in eastern sites) and a higher mean DSH (52.7 cm vs 25.3 cm in eastern sites).

Discussion

Understanding how the factors that influence Douglas-fir beetle population dynamics differ between eastern and western Washington Douglas-fir forests is complex but necessary as the climate continues to change across the region. Through this multi-year field study, I observed that many of the relationships between Douglas-fir beetle abundance and statistically important predictor variables were similar across eastern and western Washington, but important differences do exist. Contrary to my hypothesis that natural enemy communities are more abundance and diverse in coastal Douglas-fir forests, the natural enemy community is more abundance and diverse in eastern sites. The overall lower abundance of endemic Douglas-fir beetle populations at all western sites, and subsequently lower abundance of natural enemies, suggests that natural enemies are not applying top-down pressure. Instead, natural enemies appear to be numerically responding to the size of the Douglas-fir beetle population. Similar to past research (Negron 1998), the abundance of Douglas-fir beetle increased with the proportion of Douglas-fir basal area, but only in western sites where population densities were much lower, refuting my hypothesis that that a lack of suitable host trees is limiting Douglas-fir beetle outbreaks in western sites, and suggesting it is not an important factor in explaining the population differences between eastern and western sites. This also suggests that other factors, such as climate and Douglas-fir beetle outbreak proximity and size, appear to better explain the differences in the abundance of Douglas-fir beetle populations in eastern and western Washington.

Ward & Aukema (2019) showed that conspecific outbreaks were the best predictor of intraspecific forest insect activity in nearby grid cells for larch casebearer *Coleophora laricella* Hubner (Lepidoptera: Coleophora) and eastern larch beetle *Dendroctonus simplex* LeConte (Coleoptera: Curculionidae) on a common host, tamarack *Larix laricina* (Du Roi) Koch (Pinaceae). Consistent with this finding, I observed that Douglas-fir beetle abundance was greater in sites that were closer to the nearest conspecific outbreak. Though this pattern appears to be more extreme in eastern Washington (Fig. 5C), the western Washington site at the University of Washington Center for Sustainable Forestry at Pack Forest was >40 km away from the nearest Douglas-fir beetle outbreak. However, because aerial surveys in 2020 were limited due to COVID 19 restrictions, it is possible that outbreaks closer in space were not recorded (USDA Forest Service 2019). When excluding this possible artificially high distance between outbreaks, similar patterns of greater Douglas-fir beetle abundance were observed in eastern and western sites that were closer to conspecific outbreaks. Similarly, there was a signal of increasing Douglas-fir beetle abundance as the size of the nearest outbreak increased in western Washington (Fig. 5D). The relationship of Douglas-fir beetle abundance and size of nearest outbreak in eastern Washington was more nuanced with a peak in abundance in sites that were near conspecific outbreaks roughly 60 hectares in size, suggesting that smaller outbreaks may provide less propagule pressure for nearby outbreaks, but larger outbreaks may result in intraspecific competition in nearby areas. All together, these findings suggest that Douglas-fir beetle abundance in western Washington sites is limited more so by the smaller size of nearby conspecific outbreaks while the larger outbreaks serve to promote the generally higher population densities observed in eastern Washington sites.

Other irruptive bark beetle species, such as mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae) and spruce beetle *Dendroctonus rufipennis* Kirby (Coleoptera: Curculionidae), have been shown to benefit from warmer winter temperatures (Bentz et al. 2010;

Weed et al. 2015). I observed a similar relationship between warmer winter temperatures and the abundance of Douglas-fir beetle in both eastern and western Washington sites. This has important implications under changing climatic regimes as winter temperatures have shown the largest increases across the Pacific Northwestern region (Abatzoglou et al. 2014), and Douglas-fir beetle is generally not considered to be particularly cold hardy (Johnson 1967). The increase in abundance of Douglas-fir beetle in response to higher Hargreaves climatic moisture deficits in the summer on both sides of the Cascades echoes past research highlighting the role of drought conditions serving to promote bark beetle outbreaks (Powers et al. 1999; Berg et al. 2006; Howe et al. 2022). This increase is likely a result of reduced Douglas-fir defensive capacity across the region from increased underlying drought stress (van Mantgem et al. 2009; Restaino et al. 2016), and provides evidence in support of my hypothesis that greater drought stress in the interior Douglas-fir region has resulted in more susceptible host trees. Interestingly, this pattern appears to be driven largely by deficits in eastern Washington (Fig. 5H), which highlight a potential threshold at roughly 300 mm deficits where maximum deficit values end for western sites and near where they begin for eastern sites. Deficits greater than 300 mm show increases in Douglas-fir beetle abundance, but only in the already drought prone eastern sites where these higher values exist. The negative effect of mean maximum summer temperatures from the previous year on Douglas-fir beetle abundance suggests that higher summer temperatures may serve to disrupt emergence and/or dispersal (typically April - July; Jones et al. 2019; Freeman et al. 2020) by limiting flight capacity; however, it is important to note that, to the best of my knowledge, maximum flight temperature limits are unknown for Douglas-fir beetle (Jones et al. 2019). Douglas-fir beetle abundance also decreased with greater autumn Hargreaves climatic moisture deficits from the previous year, suggesting that late season drought negatively impacts beetle performance.

Douglas-fir beetle is an important component of the Douglas-fir forests of the Pacific Northwest. As climatic conditions continue to change across the region, potentially favoring the development of larger outbreaks, the role of Douglas-fir beetle as a biotic disturbance agent warrants greater attention. Although coastal Douglas-fir forests of western Washington have been historically resilient to large-scale Douglas-fir beetle outbreaks, increases in summer temperatures and drought, similar to conditions in eastern Washington, could weaken host tree vigor and facilitate Douglas-fir beetle population growth. The abundance of suitable Douglas-fir host trees across Western Washington, coupled with the low densities of Douglas-fir beetle suggests that much of this suitable host material is well defended given a reduced natural enemy community relative to eastern Washington. Moreover, anomalous weather events (e.g., windstorms, heatwaves, landslides) are projected to increase (Clarke et al. 2022; Heeter et al. 2023), which could create large pulses of susceptible host trees. When combined with potentially increased summer drought resembling eastern Washington sites, subsequent Douglas-fir beetle outbreaks in western Washington could become spatially and uncharacteristically larger, which could result in a cascading effect given the importance of the size and proximity of nearby outbreaks in eastern Washington in affecting outbreak dynamics. Further research should aim to identify if thresholds in nearby outbreak size and summer drought do indeed exist in the Douglas-fir beetle system, and, if so, attempt to predict the potential for breaching these thresholds under future climate projections. Understanding the factors that limit Douglas-fir beetle populations is vital in predicting how population dynamics may shift under changing climatic regimes. The ability to predict areas that are most vulnerable to Douglas-fir beetle under changing conditions could help promote proactive management strategies to mitigate the consequences of outbreaking Douglas-fir beetle populations.

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Tables

Table 1. List of potential predictor variables included in the initial least absolute shrinkage and selection operator (LASSO; Tibshirani 1996) analysis.

Forest metric variable descriptions
Total basal area (m^2) of all tree species in 2-11.3m fixed radius plots
Proportion of basal area (m^2) of Douglas-fir trees in 2-11.3m fixed radius plots
Tree species Shannon Diversity Index calculated by basal area (m^2) in 2-11.3m fixed radius plots
Landscape metrics variable description
Slope aspect (cardinal and intercardinal directions)
Transect slope (degrees)
Transect elevation (m)
Coefficient of variation of elevation within 10 x 10 km cell centered on site
Mean elevation (meters) within 10 x 10 km cell centered on site
Standard deviation of elevation within 10 x 10 km cell centered on site
Proximity (kilometers) of nearest Douglas-fir beetle outbreak in previous year
Size (hectares) of nearest Douglas-fir beetle outbreak in previous year
Proximity (kilometers) of nearest Douglas-fir beetle outbreak in current year
Size (hectares) of nearest Douglas-fir beetle outbreak in current year
Weather metrics variable description (Wang et al. 2016)
Mean maximum winter (December (previous year) – February) temperature at middle of transect
Mean maximum spring (March - May) temperature at middle of transect
Mean maximum winter (December (previous year) – February) temperature at middle of transect
Mean minimum spring (March - May) temperature at middle of transect
Hargreaves climatic moisture deficit in spring (March - May) at middle of transect; sum of the monthly difference between a reference evaporation (Eref) and precipitation
Hargreaves climatic moisture deficit in summer (June - August) at middle of transect; sum of the monthly difference between a reference evaporation (Eref) and precipitation
Annual heat:moisture index for previous year; ((Mean annual temperature (°C) + 10)/(Mean annual precipitation (mm)/1000)
Mean maximum spring (March - May) temperature in previous year at middle of transect
Mean maximum summer (June - August) temperature in previous year at middle of transect
Mean maximum autumn (September - November) temperature in previous year at middle of transect
Hargreaves climatic moisture deficit in previous year spring (March - May) at middle of transect; sum of the monthly difference between a reference evaporation (Eref) and precipitation.
Hargreaves climatic moisture deficit in previous year summer (June - August) at middle of transect; sum of the monthly difference between a reference evaporation (Eref) and precipitation.
Hargreaves climatic moisture deficit in previous year autumn (September - November) at middle of transect; sum of the monthly difference between a reference evaporation (Eref) and precipitation

Table 2. Coefficient estimates (± SE) for all variables selected through least absolute shrinkage and selection operator (LASSO), which were then tested for significance using two generalized linear mixed-effects models, GLMM1 which excluded side due to high multicollinearity, and GLMM2 which included side and interaction effects with side. Because data from multifunnel traps located along the same transect were likely to be autocorrelated, a random effect of transect was included in both GLMM models and evaluated with a log-likelihood ratio test using *ranova* in the *lmerTest* package (Kuznetsova et al. 2022).

Predictor	Lasso	GLMM1	GLMM2
Intercept	4.03 ± 0.04	4.69 ± 0.73***	5.46 ± 0.77***
CV of elevation	-0.77 ± 0.02	NA	NA
Proportion of Douglas-fir in basal area	0.10 ± 0.004	0.21 ± 0.10 *	-0.03 ± 0.13
Tree species Shannon diversity index	-0.02 ± 0.0004	NA	NA
Proximity of nearest DFB outbreak	-0.008 ± 9.8e-05	-0.02 ± 0.002***	-0.01 ± 0.03***
Size of nearest DFB outbreak	0.003 ± 8.5e-05	0.002 ± 0.0008*	NA
Mean minimum winter temperature (current year)	0.06 ± 0.0005	0.12 ± 0.01***	0.17 ± 0.03***
Hargreaves CMD in summer (current year)	0.003 ± 4.0e-05	0.007 ± 0.0009***	0.004 ± 0.001**
Mean maximum summer temperature (previous year)	-0.07 ± 0.002	-0.15 ± 0.04***	-0.12 ± 0.02***
Hargreaves CMD in autumn (previous year)	-0.007 ± 0.0002	NA	NA
Natural enemy species richness	0.14 ± 0.001	0.13 ±0.03***	0.12 ± 0.02***
Side (west)	NA	NA	-1.03 ± 0.33**
Interaction of Proportion of DF and Side (west)	NA	NA	0.59 ± 0.20**
Akaike Information Criterion (AIC)	NA	11.26	4.01

NA Denotes removal from final model because of high multicollinearity or p-values >0.05

* Denotes statistical significance at α = 0.05

** Denotes statistical significance at α = 0.01

*** Denotes statistical significance at α = 0.001

Figures

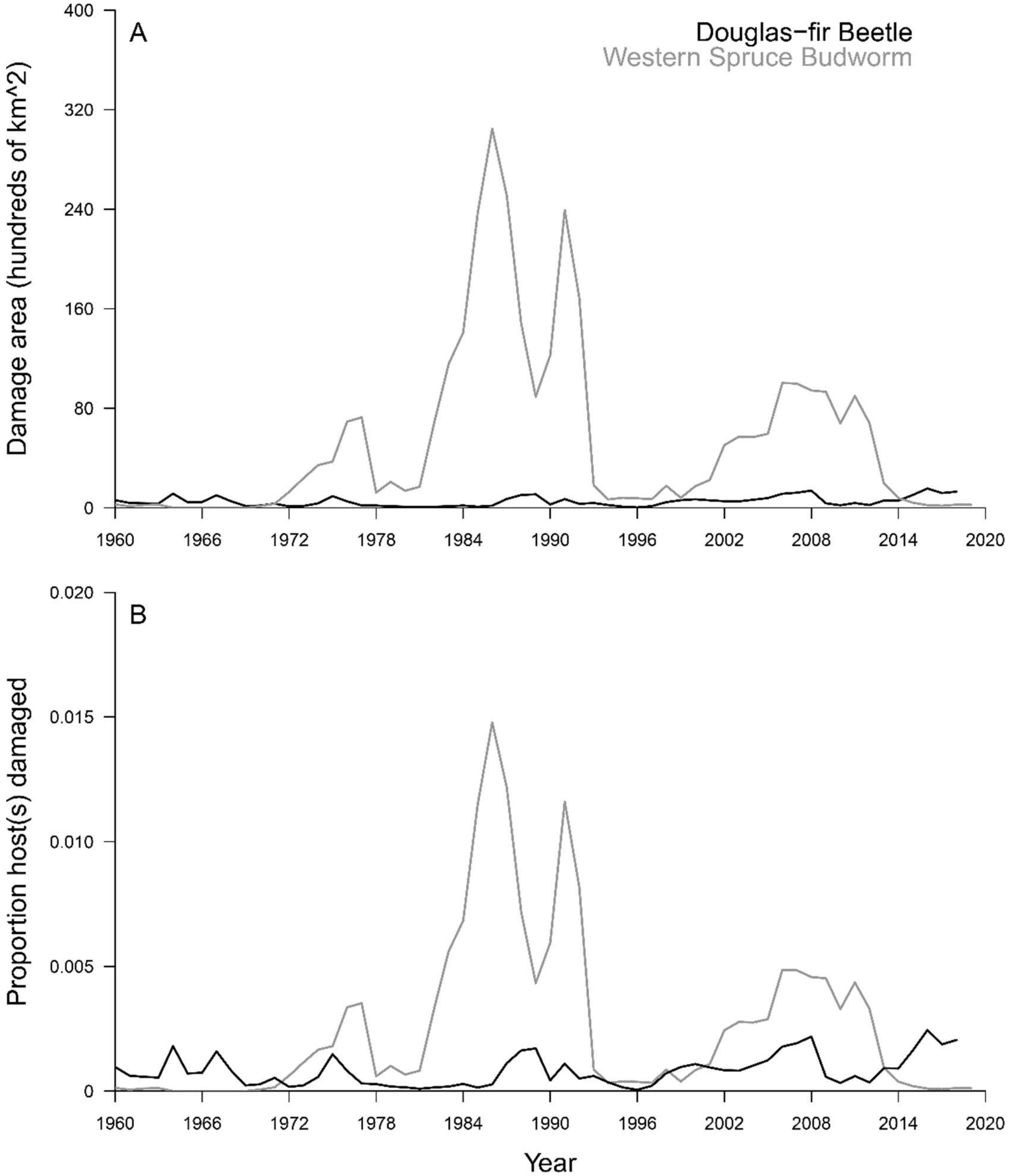

Figure 1. Total area affected (A) and proportion of host trees damaged (B) for Douglas-fir beetle and western spruce budworm, 1960-2019 in British Columbia, Washington State and Oregon. The proportion of host(s) affected was calculated by dividing the area disturbed, as recorded by aerial surveys from the British Columbia Ministry of Forests & Canadian Forest Service (2019) and the USDA Forest Service (2019) by the area of available primary host(s) tree species according to Little (1971). The annual proportion of host tree affected for each insect allows for a more standardized comparison Douglas-fir beetle primarily attacks Douglas-fir while western spruce budworm primarily attacks Douglas-fir and *Abies* spp.

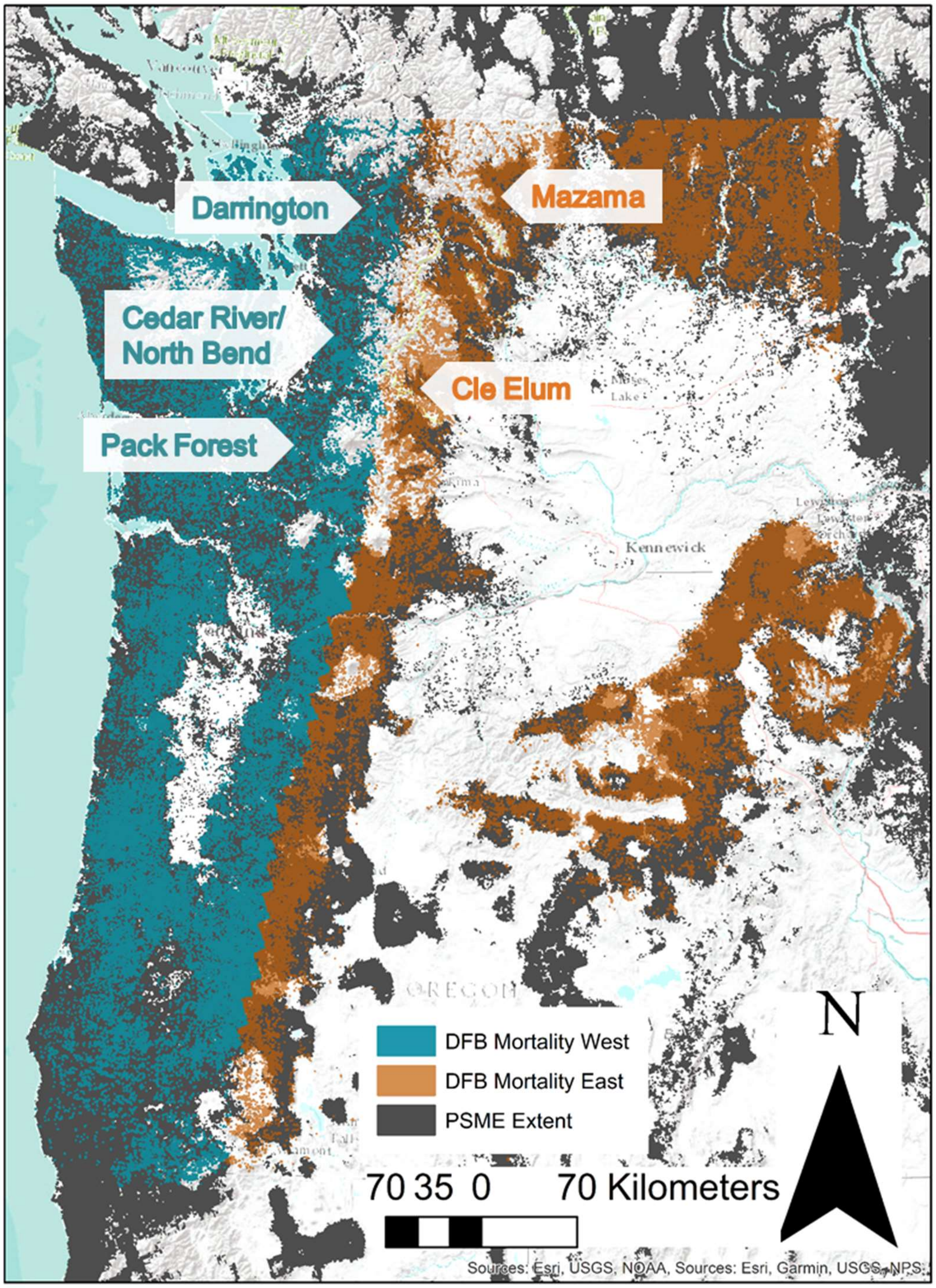

Figure 2. Study locations across western and eastern Washington, 2019-2021. Also shown is the distribution of Douglas-fir (Mathys et al. 2014), and the spatial extent of Douglas-fir beetle (DFB) mortality from 1960-2018 in Oregon and Washington (USDA Forest Service 2019). Although the area over which Douglas-fir beetle has caused some measurable level of mortality is similar in eastern and western Washington and Oregon, ~1.36 million hectares of mortality have been recorded in the east while only ~0.62 million hectares have been recorded in the west over the past 60 years (USDA Forest Service 2019).

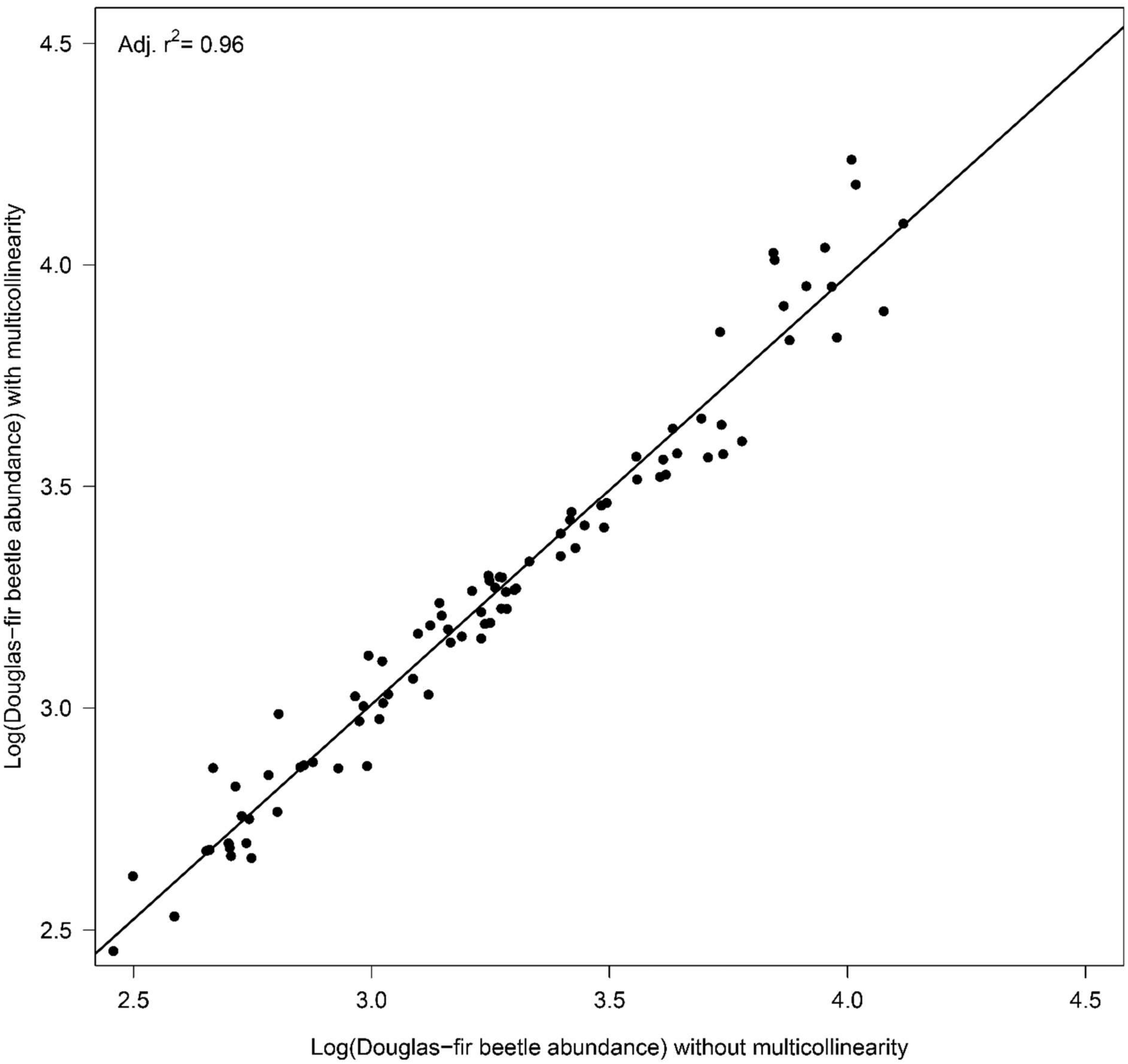

Figure 3. Least squares regression fit of the predicted log10 Douglas-fir beetle abundance from GLMM models without multicollinearity (i.e., the exclusion of a side variable denoting eastern or western Washington) and with multicollinearity (i.e., the inclusion of a side variable denoting eastern or western Washington). The regression fit had an adjusted $r^2 = 0.96$, suggesting that the multicollinearity introduced by the inclusion of a side variable did not over- or underestimate model predictions.

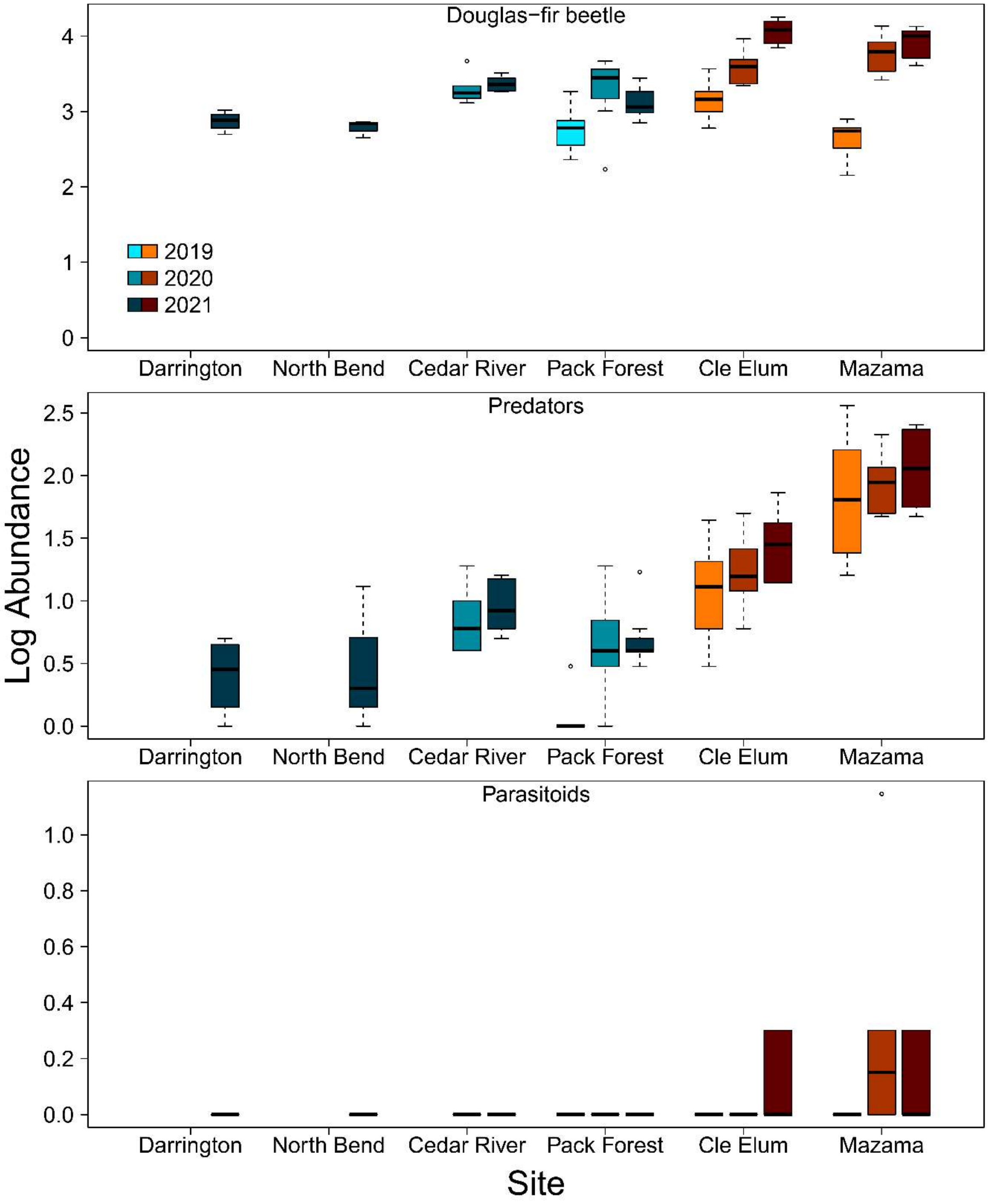

Figure 4. Boxplots of the per trap log10 abundance of Douglas-fir beetle, predators, and parasitoids for 2019, 2020, and 2021, as measured from multifunnel traps deployed with semiochemical cues mimicking the Douglas-fir beetle aggregation pheromone and host tree stress (ethanol). Blue colors indicate western Washington sites and orange colors indicate eastern Washington sites.

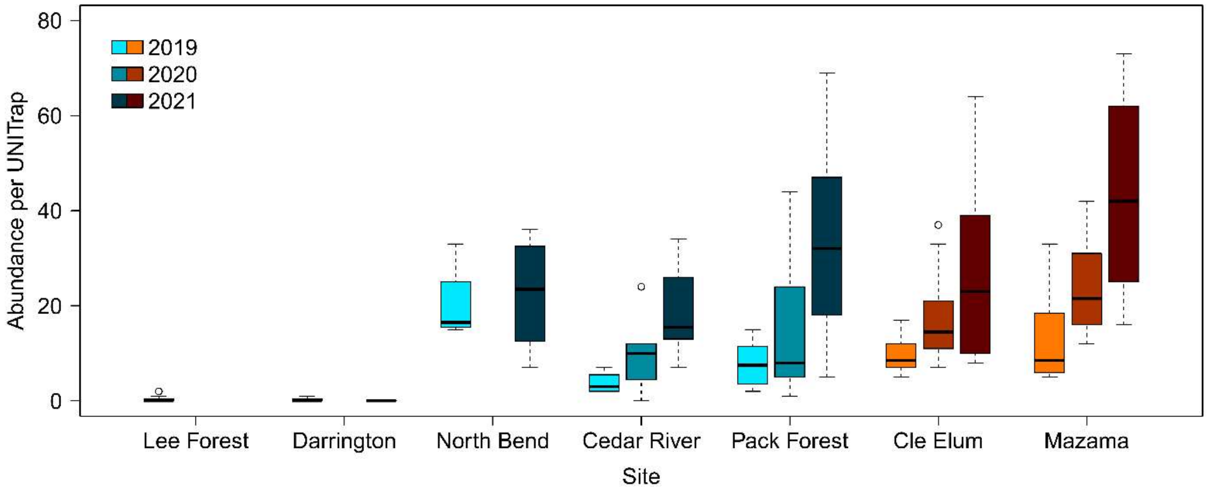

Figure 5. Boxplot of the per trap abundance of western spruce budworm for 2019, 2020, and 2021, as measured from UNI-traps deployed with the western spruce budworm sex pheromone. Blue colors indicate western Washington sites and orange colors indicate eastern Washington sites.

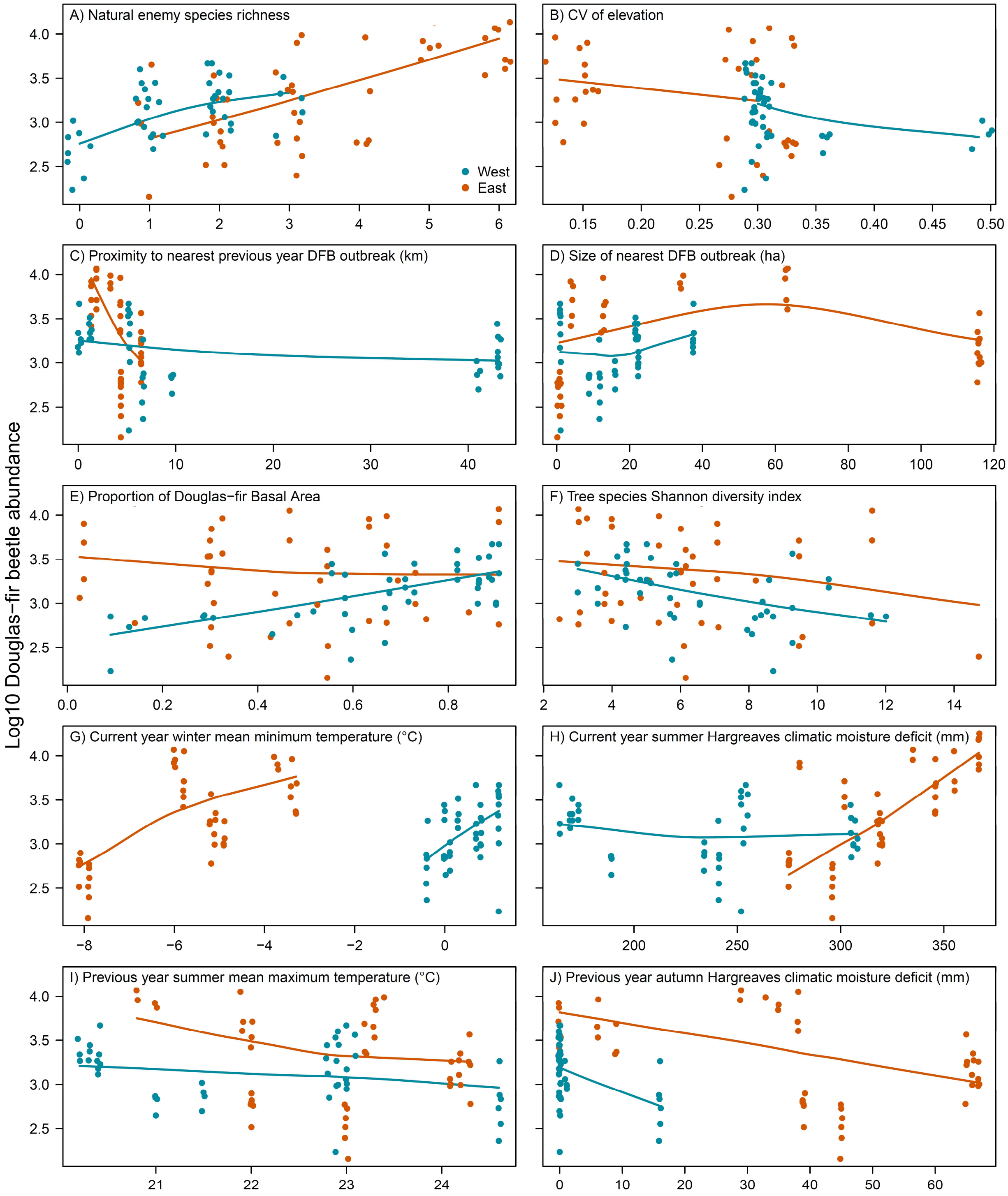

Figure 6. Relationships between the log10 abundance of Douglas-fir beetle and non-zero explanatory variables split by eastern (orange) and western (blue) Washington sites. All variables were initially selected through least absolute shrinkage and selection operator (LASSO) and subsequently tested using generalized linear mixed-effects models.

Chapter 3: The role of natural enemies and competition on the population dynamics of Douglas-fir beetle

Abstract

Some bark beetle species have the capacity, under favorable conditions, to undergo increases in population density that result in spatially-extensive outbreaks with economic and ecological consequences. However, these irruptive bark beetle species are most often constrained to endemic population levels by various biotic and abiotic factors. At low population densities, bark beetles are limited by local scale constraints such as host tree defenses and availability, subcortical competitors, and natural enemies in the form of predators and parasitoids. I investigated the role of invertebrate natural enemies and competitors in providing top-down pressure on low density Douglas-fir beetle populations in eastern and western Washington by mapping and quantifying interactions beneath the bark using ImageJ software and identifying all emerged species. Findings suggest that the robust interspecific competitor community in the interior Douglas-fir forests did not appear to play a major role in limiting Douglas-fir beetle population densities and suggests competition does not likely play a role in western Washington. *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae) was the most abundant predator among all sites and was captured predominantly in western Washington, suggesting that this species may play a key role in limiting endemic Douglas-fir beetle populations in coastal Douglas-fir forests as it prefers moister habitats. The lower *M. aldrichii* counts observed in eastern sites were bolstered by greater numbers of predaceous Coleoptera, which may perform better in the drier interior forests, but be limited in their top-down pressure on Douglas-fir beetle populations as many are generalist predators on the competing subcortical herbivorous community. Understanding the current patterns of interactions between Douglas-fir beetle and its associated

competitor and natural enemy community provides the basis for determining how these interactions may shift under the projected climate warming across the region. Preemptively treating areas where Douglas-fir beetle outbreaks are likely to become more pronounced could potentially reduce its economic and ecological impact.

Introduction

Some bark beetle species have the capacity, under favorable conditions, to undergo increases in population density that result in spatially-extensive outbreaks with economic and ecological consequences. However, these irruptive bark beetle species are most often constrained to endemic population levels by various biotic and abiotic factors. For example, at low population densities, bark beetles are limited by local scale constraints such as host tree defenses and availability (Safranyik & Carroll 2006; Raffa et al. 2008; Cooke & Carroll 2017), subcortical competitors (Coulson et al. 1976, 1980), and natural enemies in the form of predators (Cowan & Nagel 1965; Moeck & Safranyik 1984; Reeve 1997) and parasitoids (Ryan & Rudinsky 1962; Kline & Rudinsky 1964; Marsden et al. 1981). Bark beetles develop under the bark of trees in the phloem layer, making it difficult to study the influence of natural enemy pressure on population dynamics (Coulson 1979; Dahlsten 1982). Understanding the role of natural enemies in affecting bark beetle population dynamics remains an important avenue of research, particularly as some bark beetle outbreaks become more spatially extensive and damaging under changing climatic conditions (Chapter 1).

The coniferous forests of western North America are host to several bark beetle species, some of which cause widespread tree mortality with important ecological and economic consequences. One species of particular interest is Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae: Scolytinae), which caused ~2 million hectares (mha) of tree mortality in its primary host, Douglas-fir *Pseudotsuga menziesii* (Mirbel), in Washington and Oregon over the past 60 years (USDA Forest Service 2019). Douglas-fir beetle is a relatively non-aggressive bark beetle that preferentially attacks weakened and stressed Douglas-fir by boring through the bark and consuming phloem tissue (Furniss & Kegley 2014). However, it is capable of killing vigorous trees at sufficiently high population densities (Negron 1998). This behavior results in patterns of relatively small, patchy mortality events in areas that have been previously disturbed or that show signs of reduced growth (Negron 1998; Six & Skov 2009). Though large-scale outbreaks of Douglas-fir beetle are relatively uncommon in the Pacific Northwest, large and sustained (>3 years) outbreaks have been observed in the Rocky Mountains, often following widespread injury to trees by fire, drought, pathogens, and/or defoliation (Furniss et al. 1979; Hadley & Veblen 1993; Ryan & Amman 1996; Powers et al. 1999; Cole et al. 2022).

The climate of the western Cascade Range is typified by moist, mild winters and summer drought conditions (Franklin & Dyrness 1988). The climate of the eastern Cascade Range is characterized by cold, snowy winters, hot and very dry summers, and a shorter growing season (Franklin & Dyrness 1988). Additionally, the climate across the Pacific Northwest has changed over the past century, with annual mean temperatures increasing 0.6-0.8°C from 1901-2012 (Abatzoglou et al. 2014). Increasing maximum and minimum temperatures have also been observed across all seasons, with the largest increases occurring during winter months, while decreasing summer and autumn precipitation have increased climatic water deficits across the region (Abatzoglou et al. 2014). Douglas-fir beetle occurs east and west of the Cascade Mountains (Fig. 2, Chapter 2); however, there has been over twice as much Douglas-fir mortality in the east (~1.36 mha) relative to the west (~0.62 mha) (USDA Forest Service 2019). As the climate continues to warm, it is unclear whether these patterns will continue, or if tree mortality will increase in the western Cascade region.

Natural enemies, particularly invertebrate predators, have been shown to provide top-down control over endemic bark beetle populations, but have little effect on irruptive outbreaking populations due to predator satiation (Moeck & Safranyik 1984; Reeve 1997). Moreover, increases in natural enemy densities typically lag host populations in both time and space (Moeck & Safranyik 1984; Furniss & Kegley 2014). Most of the studies that identified natural enemies of Douglas-fir beetle were conducted ~60 years ago and often under disparate conditions and locations. Predators from Cleridae and Trogossitidae are perhaps the most well studied natural enemies of Douglas-fir beetle as they typically show a kairomone response to aggregation pheromones produced by adults. Consequently, these predators are often trapped in semiochemical-baited multifunnel traps used to monitor bark beetle populations (Furniss et al. 1981; Dahlsten 1982; Billings & Cameron 1984). Predators include species from Coleoptera (e.g., *Enoclerus sphegeus* (Fabricius)*, Thanasimus undatulus* (Say)*, Temnoscheila chlorodia* (Mannerheim)), Diptera (e.g., *Medetera spp., Lonchaea spp., Belosta albipilosa* Hardy), and Raphidioptera (e.g., *Agulla spp.*), which collectively attack larval and adult stages of Douglas-fir beetle (Kline & Rudinsky 1964; Johnsey et al. 1965; Marsden et al. 1981; Moeck & Safranyik 1984; Zack et al. 1998; Furniss 2014). Similar to many predators, interspecific competitors, such as woodborers within Buprestidae and Cerambycidae, and other bark beetles within Scolytinae, also show a kairomonal response to aggregation pheromones produced by bark beetles (Billings & Cameron 1984; Allison et al. 2001). Larvae of these species compete with Douglas-fir beetle larvae for nutritional resources provided by the phloem (Coulson et al. 1976; Miller 1985; Boone et al. 2008). Some woodborer larvae can also potentially serve as facultative predators in cases where foraging larvae overlap (Dodds et al. 2001). Some studies have highlighted that intraspecific competition may limit Douglas-fir populations (see Schmitz & Rudinsky 1968); however, to the best of my knowledge, none have compared the role of intraspecific in eastern and western Washington sites. Among parasitoids that attack Douglas-fir beetle, most are hymenopteran species within Braconidae (which are generally larval parasitoids; e.g., *Coeloides vancouverensis* (Dalla Torre)) and Pteromalidae (which generally parasitize adults; e.g., *Karpinskiella paratomicobia* Hagen and Caltagirone) (Ryan & Rudinsky 1962; Dahlsten 1982; Moeck & Safranyik 1984).

Chapter 2 was a critical first step to identifying potential east-west differences in the diversity and abundance of the natural enemy community interacting with Douglas-fir beetle, and suggested that natural enemies are more abundant and diverse in eastern Washington, but appear to have little effect on population densities. Additionally, the Chapter 2 approach could overestimate the role of interacting species that use Douglas-fir beetle aggregation pheromones (Billings & Cameron 1984; Allison et al. 2001; Boone et al. 2008) or ethanol, which is used as a bait in multifunnel traps, as kairomones, while underestimating the role of interacting species that respond to other cues (Ryan & Rudinsky 1962). Directly analyzing the interactions occurring under the bark could offer a more complete understanding of the communities associated with Douglas-fir beetle, and the top-down pressure they exert in eastern and western Washington populations. It remains unclear whether the natural enemy and competitor communities associated with Douglas-fir beetle exert similar top down pressure in the disparate ecosystems of the western and eastern Douglas-fir regions of Washington.

The overarching goal of this study was to evaluate the role of the natural enemy and competitor community assemblage in providing top-down pressure on Douglas-fir beetle populations. Because sociochemical-baited multifunnel traps can potentially under or over -estimate the natural enemy community, I also compared the Chapter 2 community assemblages in eastern and western Washington sites to those captured in bark samples to determine if differences are present. Although the Douglas-fir beetle natural enemy diversity and abundance east of the Cascade mountains is greater than that found in the west, the larger Douglas-fir beetle populations and higher rates of tree mortality in the former suggest that the efficacy of natural enemies in controlling beetles is lower in eastern sites. Therefore, I hypothesize that there is a greater abundance of predators per number of Douglas-fir beetle larvae, a greater proportion of parsitized larvae, a greater proportion of phloem consumed by interspecific competitors, and greater intraspecific competition, which collectively provide greater top-down pressure on Douglas-fir beetle populations in western Washington sites.

Materials and Methods

Experimental Design

In 2019, I used U.S. Forest Service aerial detection survey data (USDA Forest Service 2019) to identify four sites across Washington, two east of the Cascade Range (Cle Elum and Mazama) and two west of the Cascade Range (Cedar River and Pack Forest; Fig. 2, Chapter 2). Sites that were selected had no recorded Douglas-fir beetle outbreaks in the preceding five years, and were composed primarily of Douglas-fir, defined as >50% basal area represented by Douglas-fir (Weatherby & Thier 1993; Freeman et al. 2020). At each site in 2019, 2020, and 2021, I felled 1-2 healthy Douglas-fir trees ~35cm diameter at standard height (DSH, ~1.4 m from the ground) in late April to early May before peak Douglas-fir beetle flight (Freeman et al. 2020) to serve as trap trees. In 2020, due to COVID-19 restrictions, I was not able to sample in the two eastern Washington sites; overall, there were a total of 21 site-years.

Felled trees were left for one year to allow Douglas-fir beetle and any natural enemies and competitors to colonize the tree and complete development. In late April to early May the following year, before Douglas-fir beetles complete their development, attacked portions of the bark along the bole were stripped and placed in emergence containers under laboratory conditions (~20°C, 75% humidity, and natural light; Figs. 1A & B) to allow Douglas-fir beetles, competitors, parasitoids, and predators to complete development and emerge. Most (>95%) natural enemies and competitors that emerged (Figs. 1C & D) were identified to species using microscopy with reference keys and photographs from several sources (Ryan & Rudinsky 1962; Kline & Rudinsky 1964; Cowan & Nagel 1965; Johnsey et al. 1965; Marsden et al. 1981; Dahlsten 1982; Moeck & Safranyik 1984; Aspöck 1986; Bright 1987; Evans & Hogue 2006; Goheen & Willhite 2006; Furniss 2014). Some species could only be identified to genus, but this represented only ~4% of the total number of emerged adults.

Quantifying Douglas-fir Beetle Interactions with Natural Enemies and Competitors

A photograph (72 DPI) of each bark sample was taken before being placed in emergence containers (Fig. 1). A total of 424 and 186 bark samples (~550 cm^2 in area on average) were taken and photographed across all years in western and eastern sites, respectively, from which 238 (west) and 170 (east) samples were used in this study. The remainder of bark samples could not be assessed because of extensive rot or poor photograph quality (e.g., blurry photo, poor lighting), making it difficult to quantify subcortical larval activity. The subset of photographs were then analyzed using ImageJ software (Schneider et al. 2012). ImageJ software is an image processing program that offers many tools for measuring and quantifying distinguishable features of an image, which allowed me to quantify various Douglas-fir beetle, natural enemy, and competitor metrics. Bark beetle and woodborer activity under the bark can be readily distinguishable as the gallery patterns from different species of subcortical feeders are quite distinct (Furniss & Johnson 2002). Similarly, parasitized bark beetle larvae can be feasibly differentiated from unparasitized larvae, even after the parasitoid has emerged.

Image analysis began with setting the scale using an object of known length (e.g. adult Douglas-fir beetle, which is ~5.1 mm, or the width of the Douglas-fir beetle maternal gallery, which is ~ 5.4 mm). These values were estimated by measuring 60 randomly selected Douglas-fir beetle adults and 740 randomly maternal galleries, and then calculating the mean for each. With the scale set in mm, measurements were taken using the polygon selections and line tools, then saved as an image overlay to maintain a record of what was included in each measurement (Table 1, Fig. 1E). Measurements and counts were then used to calculate a performance metric for Douglas-fir beetle, which was calculated as the proportion of phloem area occupied by Douglas-fir beetle divided by the number of Douglas-fir beetle larval gallery starts. Other measurements included total phloem area (mm^2), phloem area occupied by Douglas-fir beetle (mm^2), phloem area occupied by woodborers (mm^2), phloem area occupied by other bark beetles (i.e., other Scolytinae; mm^2), phloem area jointly occupied by Douglas-fir beetle and woodborers (mm^2), the number of Douglas-fir beetle maternal galleries, the number of parasitized Douglas-fir beetle larvae, and number of Douglas-fir beetle larval gallery starts. The phloem area occupied by only woodborers, by only other bark beetle species, and when woodborers overlap with Douglas-fir beetle, allows for estimation of competition with Douglas-fir beetle for phloem resources. The number of parasitized Douglas-fir beetle larvae when standardized by the total number of Douglas-fir beetle larval starts provides the proportion of larvae affected by parasitoids. The number of Douglas-fir beetle maternal galleries was used to estimate an attack density per unit area when divided by the total phloem area, and allowed for estimation of potential intraspecific competition when compared to the total number of larval starts per maternal gallery (Schmitz & Rudinsky 1968; Raffa & Berryman 1983). Unfortunately, predation rates on Douglas-fir beetle could not be directly estimated with the ImageJ analysis, but the number of emerged predators per Douglas-fir beetle larval gallery starts was used as a proxy to estimate the predation rate.

Statistical Analysis

To evaluate my hypothesize that natural enemies and competitors collectively provide greater top-down pressure on Douglas-fir beetle populations in western than eastern Washington sites, I used a generalized linear model to identify the role that multiple competition, predation, and parasitization metrics play in affecting Douglas-fir beetle performance east and west of the Cascade Range. Calculations of Douglas-fir beetle performance were transformed using a square root transformation to normalize the response variable. I first considered a full model containing all predictor variables and two-way interactions with side (east or west) as fixed effects (Table 1).

Predictor variables were iteratively removed based on multicollinearity and p-values to identify the most parsimonious model in R (R Core Team 2022). Multicollinearity between fixed effects was first evaluated by calculating variance inflation factors (VIF) with the *car* package (Fox et al. 2019), resulting in the iterative removal of the variable with the highest value until all variables had a VIF < 10 (Montgomery et al. 2012). Next, the variable with the highest p-value was removed in each iteration until only variables with p-values < 0.05 remained. Using the same approach above, I also evaluated the potential role of intraspecific Douglas-fir beetle competition and side (east or west) on the number of Douglas-fir beetle larval gallery starts per maternal gallery. The main effects of attack density (i.e., number of maternal galleries per m^2) and side, and the interaction effect of attack density and side, were collectively used to estimate intraspecific competition (Raffa & Berryman 1983).

In addition to the generalized linear model, I used a two-sample Wilcoxon rank sum test to further evaluate how individual Douglas-fir beetle, natural enemy, and competitor metrics differ between eastern and western Washington sites. The Wilcoxon rank sum test compares whether two samples (east or west in this case) are from the same population by comparing the median values (need to add citation). The non-parametric test was used because many of the metrics were not normally distributed and attempts to normalize the data through transformations were not successful, in part due to the extreme bimodal distribution in the data. Variables such as the effect of competition on Douglas-fir beetle performance contained multiple metrics in the calculations (Table 1), which may also limit our comprehension of the role each individual metric serves. Further analysis of how the individual metrics that comprise these performance metrics differ between eastern and western sites could provide a greater understanding of the role each potentially play in affecting Douglas-fir beetle performance.

Results

Douglas-fir beetle was found at all sites and in all years in which bark sampling occurred (Fig. 2A). Across all years, a total of 1,861 and 333 Douglas-fir beetle adults emerged from all bark samples collected from western and eastern Washington, respectively, though samples were not taken from eastern sites in 2020. There was a greater number of trees and site-years in western Washington; thus, when Douglas-fir beetle abundance was standardized by the number samples, there was no significant difference between eastern and western sites (Fig. 3A). However, the proportion of phloem occupied by Douglas-fir beetle was statistically greater in western sites (Fig. 3B), and overall Douglas-fir beetle performance was greater in western sites (Fig. 3C). Although there was no significant difference between the proportion of overlap between woodborers and Douglas-fir beetle (Fig. 3D), the proportion of phloem area occupied by woodborers (Fig. 3E), and separately by other bark beetles (Fig. 3F), were significantly greater in eastern Washington sites.

I also recorded and identified a total of 193 predators, 208 parasitoids, and 5 competitors from western sites, and 169 predators, 73 parasitoids, and 738 competitors from eastern sites. There were no significant differences in the parasitoid abundance (Fig. 3G), number of parasitized Douglas-fir beetle larvae (Fig. 3H), or predator abundance (Fig. 3I) between eastern and western Washington sites. However, the median species richness of emerged predators was statistically greater in eastern than western Washington sites (Fig. 3J). The parasitoid *Coeloides vancouverensis* (Dalla Torre) (Hymenoptera: Braconidae) and the predator *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae) were the most abundant natural enemies in western Washington (208 and 178 individuals, respectively; Table 2). *Coeloides vancouverensis* was also one of the most abundant natural enemies in eastern Washington (73 individuals), and *Temnoscheila chlorodia* (Mannerheim) (Coleoptera: Trogossitidae) was the most abundant predator with 52 emerged individuals. The number of emerged woodboring and bark beetle competitors was much greater in eastern than western sites with only five five observed Cerambycidae larvae recorded from in western sites over 3 years of sampling (Table 2). Parasitoid wasps from *Pristaulacus* (Hymenoptera: Aulacidae) emerged from all sites, which are known to attack woodboring Cerambycidae and Buprestidae larvae (Furniss & Carolin 1977). Wilcoxon rank-sum tests of species richness and diversity of natural enemies and competitors in eastern and western Washington showed that eastern sites have significantly richer (Fig. 3K) but not significantly more diverse (Fig. 3L) communities than western sites.

After accounting for multicollinearity and eliminating nonsignificant predictor variables, the final model predicting Douglas-fir beetle performance included the effect of competition on Douglas-fir beetle performance, parasitoid abundance, natural enemy and competitor diversity, side, and the interaction terms between competition and side, and natural enemy and competitor diversity and side (Table 3). Based on the model output, Douglas-fir beetle performance was higher in western sites (Table 3). A negative effect of competition on Douglas-fir beetle performance was observed in eastern sites, but a positive relationship was observed in western sites (i.e., sites with higher Douglas-fir beetle performance metrics also had more pressure from competitors; Table 3). A negative effect of natural enemy species diversity on Douglas-fir beetle performance was only present in western Washington sites (Table 3). A positive effect of emerged parasitoid abundance on Douglas-fir beetle performance was observed across all sites, regardless of side (Table 3). Evaluating the role of intraspecific competition using the main effects of attack density and side, and their interaction, on the number of Douglas-fir beetle larval gallery starts per maternal gallery revealed that only attack density was a significant predictor (estimate = -0.16 ± 0.08, F = 4.19, df = 1, 19; p = 0.05) from which there was a negative relationship between attack density and the number of larval galleries regardless of side.

Discussion

Understanding how the natural enemy and competitor community influences Douglas-fir beetle performance in eastern and western Washington is an important avenue of research as the climate continues to change. Through this multi-year field study, I observed that there is considerable overlap between these communities in eastern and western sites, but the potential role that each guild plays on Douglas-fir beetle populations appears to be different. The non-significant trend of higher abundance of emerged Douglas-fir beetle (Fig. 3A) coupled with the significantly greater Douglas-fir beetle performance (Table 3, Fig. 3B) in western Washington sites relative to eastern sites was unexpected given that the average trap catch from multifunnel traps (Chapter 2) was 4 times greater in eastern Washington. Sites in eastern Washington were typically colder during winter and had more snow accumulation, which delayed bark removal and potentially allowed adult Douglas-fir beetles to emerge prior to sampling. However, the proportion of phloem area occupied by Douglas-fir beetle was still higher in western Washington sites (Fig. 3B), suggesting that there was in fact more Douglas-fir beetle activity in downed Douglas-fir trees in the west. The greater competitor activity observed in eastern sites (Figs. 3E & F) suggests that competition does decrease Douglas-fir beetle performance under the bark (Table 3), while lower competitor activity may explain the greater Douglas-fir beetle performance in western sites (Table 3). Furthermore, the site with the greatest amount of competition, Mazama in eastern Washington in 2021 (Fig. 2D), was located between the Cedar Creek & Cub Creek fires, which collectively burned >50,585 hectares in 2021. Woodborers positively respond to fire, taking advantage of the pulse in defensively compromised trees (Bright 1987; Ray et al. 2019; Kitchens et al. 2022), which may explain the greater competition from woodborers in fire prone eastern Washington sites. Although competition was greater in eastern sites, it does not appear to be limiting overall Douglas-fir beetle population densities (Chapter 2).

The observed greater species richness of predators in eastern sites suggests that there is a potentially more robust community preying on Douglas-fir beetle under the bark. This richer predator community in eastern Washington could be a response to the greater number of woodborers and bark beetles competing for resources under the bark as many predaceous beetles are known to prey on multiple species of subcortical larvae (Cowan & Nagel 1965; Dahlsten 1982; Moeck & Safranyik 1984; Boone et al. 2008). However, the abundance of predators was similar in eastern and western Washington, highlighting that even though there were more species captured in eastern sites, many of these species were found at low densities and unlikely played a role in limiting Douglas-fir beetle populations. Moreover, the high number of predaceous *Medetra aldrichii* observed in western sites, which prefer moist conditions (DeLeon 1935), suggests that it potentially plays a key role in low density Douglas-fir beetle populations in western Washington, as reported in past studies on Douglas-fir beetle (Johnsey et al. 1965), and other bark beetles (DeLeon 1935; Furniss & Carolin 1977). *Coeloides vancouverensis* was the only known parasitoid of Douglas-fir beetle larvae to emerge over all site-years and was most abundant in sites associated with higher Douglas-fir beetle performance, suggesting a minimal potential top-down impact not specific to eastern or western sites. Most other parasitoids of Douglas-fir beetle attack colonizing adults (e.g., Pteromalidae; Moeck & Safranyik 1984) and likely were not captured in the bark samples. Natural enemy and competitor diversity negatively affected Douglas-fir beetle performance in western sites, but had no effect in eastern sites (Table 3), providing evidence that natural enemies appear to exert greater top-down pressure on Douglas-fir beetle populations in western sites where densities are consistently lower (Chapter 2).

The richness and diversity of natural enemies captured using semiochemical-baited multifunnel traps (Chapter 2) and bark sampling revealed that bark samples allow for direct measures of community interactions with Douglas-fir beetle, particularly for species that do not show a strong kairomonal response to semiochemicals, providing context to the more general community results obtained from multifunnel trapping. Moreover, multifunnel traps capture much higher rates of predaceous Coleoptera, particularly in eastern sites where they are more abundant (Table 2). For example, a total of 2,277 *Thanasimus undatulus* and *Enoclerus sphegeus* predatory beetles were captured in multifunnel traps in eastern Washington sites (Chapter 2), but only 8 individuals emerged from bark samples taken from eastern sites (Table 2). Contrarily, competitors, parasitoids, and predaceous flies were more often recorded from bark sampling. The parasitoid *C. vancouverensis* was present in all sites where bark samples were taken, but only found at low densities in eastern sites with multifunnel traps. Similarly, *M. aldrichii* emerged in all sites where bark samples were taken (Table 2) but was not found in multifunnel traps. Altogether, these findings suggest that generalist natural enemies, such as the predaceous beetles observed in eastern sites (Cowan & Nagel 1965; Dahlsten 1982; Moeck & Safranyik 1984; Boone et al. 2008), are potentially responding to the greater diversity of subcortical herbivores interacting with Douglas-fir beetle, which may help explain their apparent lack of top-down pressure in these areas as their feeding is diluted across many species. Furthermore, the abundance of the generalist predator (DeLeon 1935; Johnsey et al. 1965), *M. aldrichii*, and the more specialized parasitoid (Ryan & Rudinsky 1962), *C. vancouverensis*, in western sites suggests that these species may provide greater top-down pressure on Douglas-fir beetle in these areas as there was a paucity of competition under the bark from western sites. Estimates of competition from multifunnel trap captures were uncertain at best as many woodboring species attack multiple host trees (Bright 1987), suggesting that they were not included in analyses from Chapter 2.

Comparing the drivers of endemic Douglas-fir beetle population dynamics in areas that show different propensities for outbreaks offers insights into potential risks as the climate and forests continue to change. Although there was a paucity of competitive pressure in coastal Douglas-fir forests, the robust interspecific competitor community in the interior Douglas-fir forests did not appear to play a major role in limiting population densities, suggesting competition would not likely play a role in western Washington. Contrary to the findings in Chapter 2, the natural enemy community is equally diverse in eastern and western sites, though the composition is considerably different. *Medetera aldrichii* was the most abundant predator among all sites and was captured predominantly in western Washington, suggesting that this species may play a key role in limiting endemic Douglas-fir beetle populations in coastal Douglas-fir forests. DeLeon (1935) found that *M. aldrichii* was an effective predator of *D. ponderosae* and tended to abandon trees that showed signs of desiccation following bark beetle attack, which is consistent with these findings suggesting supports that the drier conditions characteristic of interior Douglas-fir forests may limit the effectiveness of *M. aldrichii* in eastern sites. These lower *M. aldrichii* counts observed in eastern sites are bolstered by greater numbers of predaceous Coleoptera, which may perform better in the drier interior forests as few were captured in western sites. Understanding the current patterns of interactions between Douglas-fir beetle and its associated competitor and natural enemy community provides the basis for determining how these interactions may shift under the projected climate warming across the region. Future studies should model the potential for these trophic interactions to change under different climate projections to identify if and when these interactions may change. Preemptively treating areas where Douglas-fir beetle outbreaks are likely to become more pronounced could potentially reduce its economic and ecological impact.

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Tables

Table 1. Descriptions and calculations of all variables included in the full generalized linear model.

Response variable description
Douglas-fir beetle performance per site calculated as (phloem area occupied by Douglas-fir beetle/ total phloem area)/ number of Douglas-fir beetle larval gallery starts

Predictor variable descriptions
Effect of competition on Douglas-fir beetle performance per site calculated as: (phloem area occupied by woodborers + Area of woodborer and Douglas-fir beetle overlap + Area of other bark beetle activity)/ total area of phloem/ total number of Douglas-fir beetle larval gallery starts
Effect of predation on Douglas-fir beetle performance calculated as: total number of predators/ total number of Douglas-fir beetle larval gallery starts
Effect of parasitization on Douglas-fir beetle performance calculated as: sum of emerged parasitoids/ total number of Douglas-fir beetle larval gallery starts
Natural enemy and competitor species richness of all predators, parasitoids, and competitors of Douglas-fir beetle per site
Natural enemy and competitor Shannon diversity index of all predators, parasitoids, and competitors of Douglas-fir beetle per site
Abundance of emerged parasitoids per site
Abundance of emerged predators per site
Side (east of west) of Cascade Mountain Range

Table 2. Abundance of Douglas-fir beetle, and its competitors, parasitoids, and predators across western and eastern sites in 2019, 2020 (for western sites), and 2021.

	Western Sites		Eastern Sites	
Species	Cedar River	Pack Forest	Cle Elum	Mazama
Dendroctonus pseudotsugae Hopkins	211	1650	158	175
Competitors	—	—	—	—
Phaenops drummondi (Kirby)	0	0	8	83
Phaenops californica (Van Dyke)	0	0	0	1
Anthaxia sp.	0	0	2	18
Buprestidae larvae	0	0	18	175
Cerambycidae larvae	0	5	4	66
Scolytus unispinosus LeConte	0	0	0	4
Scolytus monticolae (Swaine)	0	0	0	366
Parasitoids	—	—	—	—
Coeloides vancouverensis (Dalla Torre)	165	43	59	14
Predators	—	—	—	—
Medetera aldrichii Wheeler	67	112	3	18
Lonchaea furnissi McAlpine	0	2	1	41
Temnoscheila chlorodia (Mannerheim)	0	4	21	31
Enoclerus sphegeus (Fabricius)	2	0	0	3
Enoclerus lecontei (Wolcott)	0	3	0	0
Thanasimus undatulus (Say)	0	0	2	3
Cleridae larvae	0	0	15	25
*Agulla sp.**	1	2	2	4

*Individuals identified to genus but species is likely *Agulla bicolor* (Albarda) based on distributional records (Aspöck 1986; Zack et al. 1998).

Table 3. Coefficient estimates (± SE) for all variables included in the final generalized linear model fit to Douglas-fir beetle performance. Variable descriptions can be found in Table 1.

Predictor	GLMM1
Intercept	0.0026 ± 0.0057
Competition effect on Douglas-fir beetle performance	-0.022 ± 0.0062**
Sum of emerged parasitoids	0.00017 ± 0.000069*
Natural enemy and competitor Shannon diversity index	0.0026 ± 0.0057
Sidewest	0.048 ± 0.0065**
Competition:Sidewest	10.97 ± 2.89**
Natural enemy and competitor diversity:Sidewest	-0.0074 ± 0.0023**

* Denotes statistical significance at $\alpha = 0.05$

** Denotes statistical significance at $\alpha = 0.01$

*** Denotes statistical significance at $\alpha = 0.001$

Figures

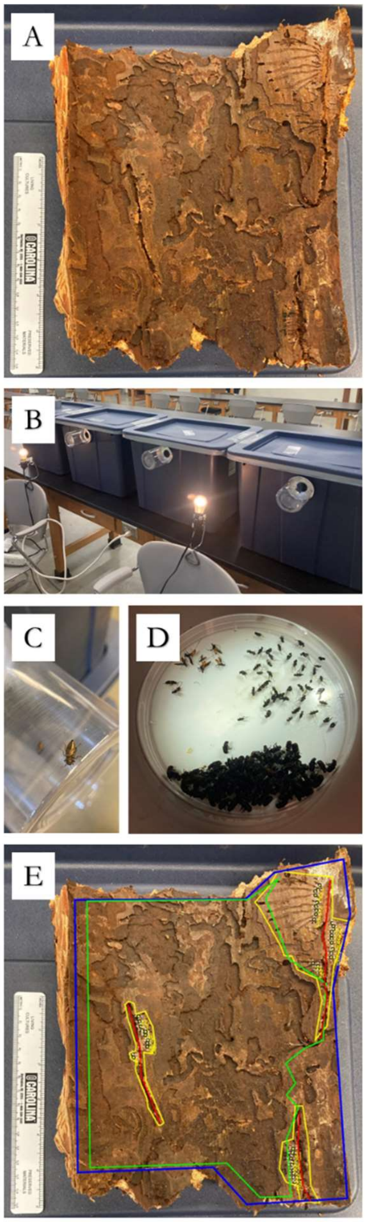

Figure 1. Bark sampling process showing bark samples (A), emergence containers (B), emerged competitors (C), Douglas-fir beetle (bottom D), parasitoids (top left D), and predators (top right D), and ImageJ analysis overlay (E). ImageJ software is an image processing program (Schneider et al. 2012) that was used to quantify Douglas-fir beetle, competitors, and parasitoid performance (Calculations available in Table 1).

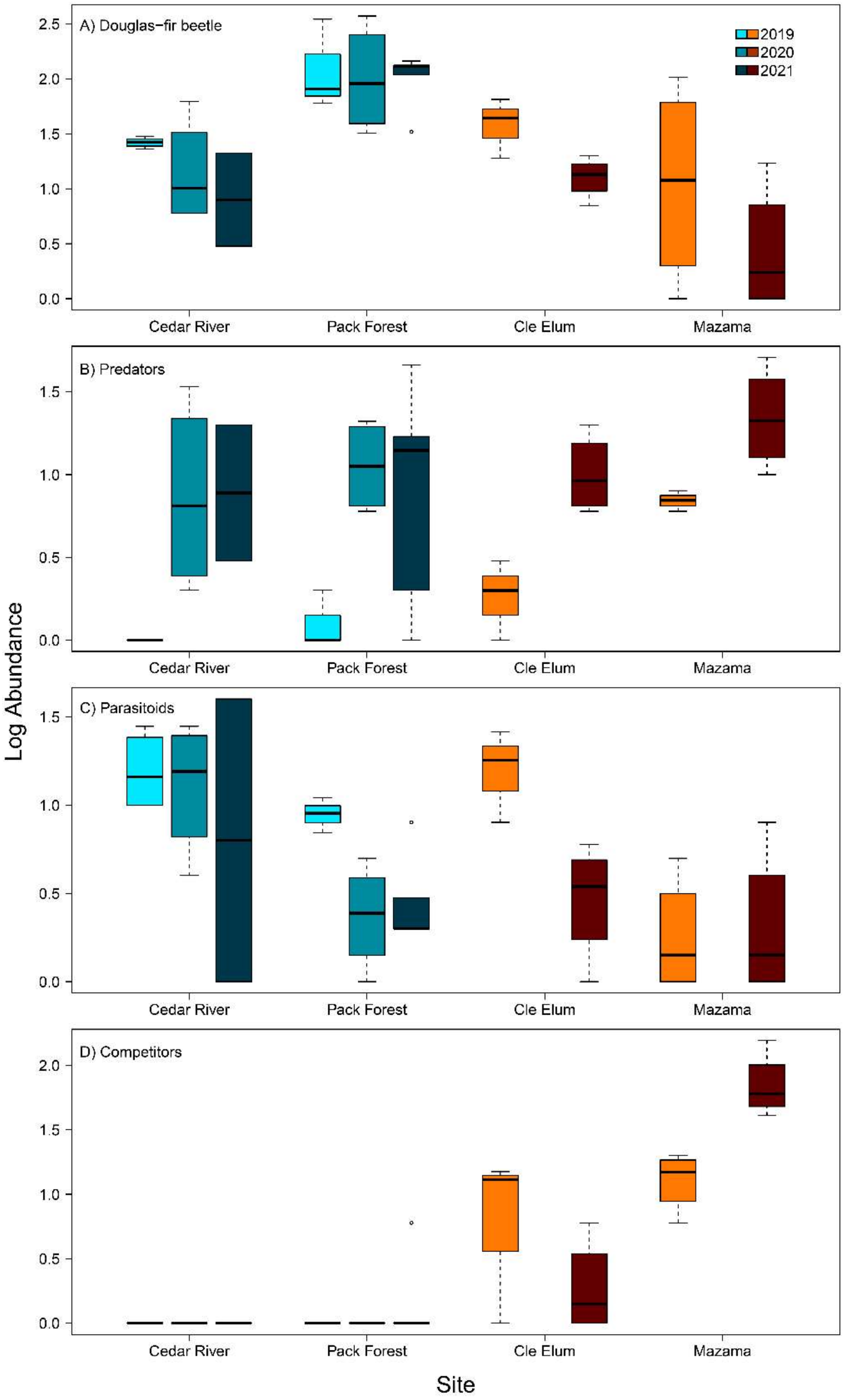

Figure 2. Boxplot of the log10 abundance of Douglas-fir beetle, predators, parasitoids and competitors from three years of bark sampling across Washington. Blue colors indicate western Washington sites and orange colors indicate eastern Washington sites. Mazama and Cle Elum sites were inaccessible due to COVID-19 restrictions, preventing bark sampling in 2020.

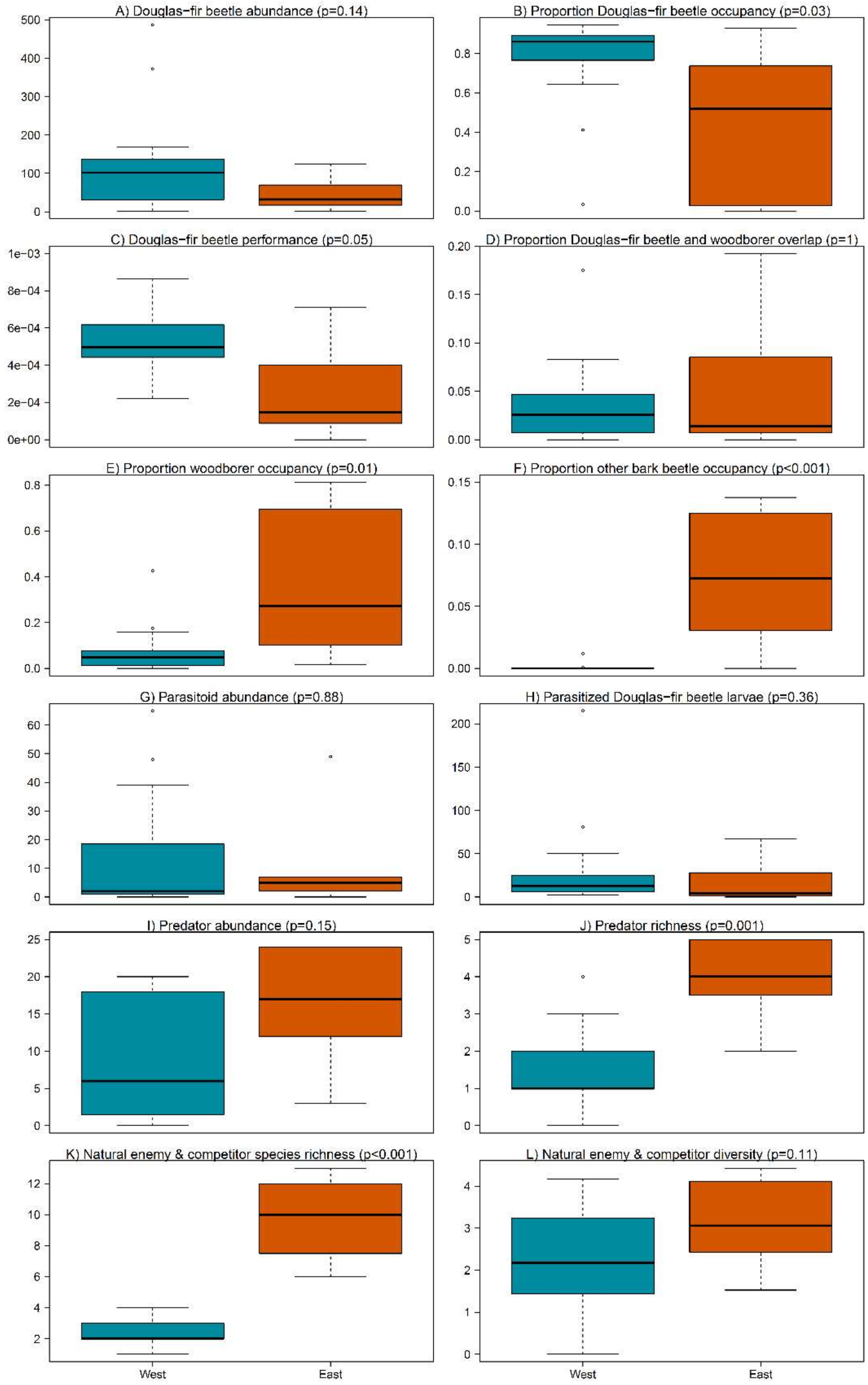

Figure 3. Boxplots comparing various Douglas-fir beetle, natural enemy, and competitor metrics among eastern and western Washington sites. The resulting p-values (in each panel title) are from two-sample Wilcoxon rank sum tests comparing each metric between eastern and western Cascade Range sites.

Chapter 4: Conclusion and synthesis

Understanding the outbreak dynamics of forest insects through the lens of a changing climate remains a complex frontier in ecology. Past research has shown that some insect species benefit from warming conditions while others are hindered. This research has highlighted that forest insect species inhabiting historically colder environments show the greatest propensity for change over the past 60 years in the Pacific Northwest. These changes are likely a result of regional warming trends as they occur over multiple species and feeding guilds, but the influence of other anthropogenic factors like fire suppression and timber harvesting cannot be ruled out. Greater spatial overlap of bark beetle and defoliator outbreaks were also observed in more recent decades, providing further evidence that climate warming is a potential factor as increases were observed across a range of climatic envelopes and potentially interacting species. Further research should aim to understand the mechanisms driving these observed changes and seek to understand how they may change under future climatic conditions.

Looking ahead, greater drought stress from this warming will likely promote greater bark beetle caused tree mortality as tree defensive capacity is compromised. Although coastal Douglas-fir forests of western Washington have been historically resilient to large-scale Douglas-fir beetle outbreaks like those seen in the southern Rockies, increases in summer temperatures and drought could weaken host tree vigor and facilitate Douglas-fir beetle population growth. The abundance of suitable Douglas-fir host trees across Western Washington, coupled with the lower densities of Douglas-fir beetle suggests that much of this suitable host material is currently well defended. However, anomalous weather events (e.g., windstorms, heatwaves, landslides) are projected to increase (Clarke et al. 2022; Heeter et al. 2023), which could create large pulses of susceptible host trees. When combined with potential increased summer drought resembling eastern Washington sites, subsequent Douglas-fir beetle outbreaks in western Washington could become spatially and uncharacteristically larger, which could result in a cascading effect given the importance of the size and proximity of nearby outbreaks in eastern Washington in affecting outbreak dynamics. Moreover, warmer and drier conditions could disrupt the top down pressure *M. aldrichii* exerts on Douglas-fir beetle populations in western Washington sites, which lacked a robust competitor community and had fewer species of predaceous Coleoptera than eastern sites.

Increasing drought stress may also reduce the nutritional content of the overall tree during chronic or severe drought events, potentially limiting population growth, particularly in the already drought prone interior Douglas-fir forests of eastern Washington. Further, high intensity fire is also projected to continue increasing as it gets warmer and drier across the region, which will likely limit insect outbreaks in general as potentially suitable and susceptible trees are removed from the system. Greater overlapping bark beetle activity, drought stress, and high intensity fire will all likely constrain the potential for defoliator outbreaks as these disturbances reduce the availability and nutritional quality of suitable host material. Further research should aim to identify if thresholds in nearby outbreak size and summer drought do indeed exist in the Douglas-fir beetle system, and, if so, attempt to predict the potential for breaching these thresholds under future climate projections.

Bark beetles and defoliators are an important component of the forests of the Pacific Northwest. As the climatic conditions continue to change across the region, potentially favoring the development of larger outbreaks with greater overlap, the role of these species as disturbance agents warrants greater attention. The changes observed in the outbreak dynamics of many species can be linked to changes in climate because insect development and reproduction are regulated by temperature. Understanding insect outbreak dynamics and their interactions over broad spatial and temporal scales, identifying the top-down and bottom-up factors influencing these changes, and quantifying how these patterns may change under a warming climate is vital to developing effective management plans for forest ecosystems.