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Balsam Woolly Adelgid and Host Forest Characteristics: Impacts and Interactions in Recently Invaded Areas of Northern Utah and Southeastern Idaho

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BALSAM WOOLLY ADELGID AND HOST FOREST CHARACTERISTICS:

IMPACTS AND INTERACTIONS IN RECENTLY INVADED AREAS OF

NORTHERN UTAH AND SOUTHEASTERN IDAHO

by

Grayson B. Jordan

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ABSTRACT

Balsam Woolly Adelgid and Host Forest Characteristics: Impacts and Interactions in Recently Invaded Areas of Northern Utah and Southeastern Idaho

by

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Utah State University, 2023

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Adelges piceae, commonly known as balsam woolly adelgid (BWA), is an invasive forest insect native to central and southern Europe. In 2017, it was detected in Utah for the first time. While BWA had limited impact as a pest in its native European range, it has caused considerable damage to true fir (*Abies* spp.) populations in North America, causing extensive damage. In the western North America, subalpine fir (*Abies lasiocarpa*) has been identified as a highly vulnerable host species, facing severe damage and mortality due to BWA infestation. The Engelmann spruce-subalpine fir system, one of the region's most important forest cover types, relies heavily on the presence and health of subalpine fir. With an expected increase in the severity and impact of BWA to the forests of northern Utah and southeastern Idaho, a study was undertaken to investigate ecological factors influencing BWA's impact and apply that knowledge to predict future impact.

To accomplish this, research plots were established across Utah and southeastern Idaho in BWA-infested areas. The study collected data on various stand and tree factors, including host size, observed damage and health of the trees, community composition, stand structure, and abiotic factors. The aim was to understand the relationships between these factors and the severity of BWA infestations. Additionally, the occurrence data of other pests affecting subalpine fir were gathered to explore potential interactions within the "subalpine fir mortality complex.” The study yielded significant findings. Firstly, it provided an assessment of recent BWA infestations within northern Utah and southeastern Idaho, estimating the severity and mortality levels caused by the insect. Secondly, the analysis of host and community characteristics revealed crucial insights, including the importance of stand structure in influencing the severity of BWA infestations. Moreover, the study shed light on the previously unexplored interactions between BWA and other pests such as bark beetles and root rot diseases affecting subalpine fir, emphasizing the complexity of the "subalpine fir mortality complex." These findings were then used in the creation of a hazard rating system for categorizing forests within our study area into risk levels based on forest and climate characteristics.

(103 pages)

PUBLIC ABSTRACT

Balsam Woolly Adelgid and Host Forest Characteristics: Impacts and Interactions in the Recently Invaded Areas of Northern Utah and Southeastern Idaho

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The balsam woolly adelgid (BWA), is an invasive forest insect native to central and southern Europe. In 2017, it was detected in Utah for the first time. While BWA had limited impact as a pest in its native European range, it has caused considerable damage to true fir populations in North America. In the Intermountain region, subalpine fir has been identified as the tree species most at risk of BWA infestation. Subalpine fir provides a variety of ecosystem services and is a critical component of the spruce-fir alpine forests of the area. With an expected increase in the severity and impact of BWA to the forests of the Intermountain region, a study was undertaken to investigate ecological factors influencing BWA's impact and apply that knowledge to predict future impact.

To accomplish this, over forty research plots were established across Utah and southeastern Idaho in BWA-infested areas. Data on various aspects of trees and stands, including tree size, observed damage and health of the trees, forest community composition, stand structure, and abiotic factors were collected. The aim was to understand the relationships between these factors and the severity of BWA infestations. Additionally, the occurrence data of other pests affecting subalpine fir were gathered to explore potential interactions within the "subalpine fir mortality complex." The study yielded significant findings. Firstly, it provided an assessment of recent BWA infestations within Utah and southern Idaho, estimating the severity and mortality levels caused by the insect. Secondly, the analysis of forest characteristics revealed crucial insights. It highlighted the importance of forest structure in influencing the severity of BWA infestations. Moreover, the study shed light on the previously unexplored interactions between BWA and other pests affecting subalpine fir. These findings were then used in the creation of a hazard rating system for categorizing forests within the study area into risk levels based on forest and climate characteristics.

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PREFACE

Because this thesis has been prepared in journal format, there is some redundancy between chapters. Chapters 2 and 3 will be submitted to peer-reviewed journals, Ecosphere and Forestry respectively, for publication in the near future. Each chapter has been or will be published with co-authors; as such, the pronoun "we" is used throughout the thesis.

CHAPTER 1

INTRODUCTION

Adelges piceae (Ratz.), balsam woolly adelgid (BWA) was present in North America by at least 1908 when it was first detected in Brunswick, Maine. For over one hundred years, BWA infestations have spread across various regions of the United States and Canada and, in some places, caused severe damage to true firs (*Abies* spp.), their principal hosts (Balch, 1952; Mitchell, 1966; Hain, 1988; Zilahi-Balogh et al., 2016). While severe damage and mortality due to BWA has occurred in several species of true fir, there has been substantial variability among fir hosts and geographic locations. Some drivers, such as host species and population density, have been described, but there is a lack of insight into how BWA interacts with community members of fir-dominated systems (Amman, 1970; Mitchell & Buffam, 2001). In 2017, the first detection of BWA in Utah marked significant range expansion eastward and raised concerns over the current and long-term consequences of its invasion (Alston et al., 2018).

In northern Utah, BWA primarily infests *Abies lasiocarpa* [Hook] Nutt., subalpine fir, which is widely distributed in western North America. It is a key component of Engelmann spruce (*Picea engelmannii* [Parry] Engelm.)-subalpine fir forests which are some of the most abundant and important alpine forests in western North America, and it has experienced an increased rate of mortality in the 21st century (Alexander, 1984; Smith et al., 2015). Changes from the historical structure and composition of western forests, such as increased stand density and reduced tree species diversity, and a changing climate have made them more susceptible to insect infestations and severe mortality events, including those due to bark beetle outbreaks. The subalpine fir mortality complex is made up of multiple agents, including insects, fungi, and abiotic factors, that can cause tree mortality (Lalande et al., 2020; Harvey et al., 2021). How BWA will interact with these agents on the landscape is unknown at both coarse and fine scales. Additionally, research has documented that subalpine fir is among, if not, the most susceptible true fir to BWA in western North America. These factors contribute to the concern of BWA's recent invasion and the damage it may cause to host trees, specifically subalpine fir, in northern Utah and surrounding states and raises questions about how BWA, its host tree, and stand communities interact.

References

Alexander, R. R. 1984. Silvical Characteristics of Subalpine Fir. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Amman, G. D. 1970. Phenomena of Adelges piceae Populations (Homoptera: Phylloxeridae) in North Carolina1. Annals of the Entomological Society of America 63:1727–1734.

Balch, R. E. 1952. Studies of the Balsam Woolly Aphid, Adelges Piceae (Ratz.) and its Effects on Balsam Fir, Abies Balsamea (L.) Mill. Canada Department of Agriculture, Science Service, Division of Forest Biology.

Hain, F. P. (1988). The balsam woolly adelgid in North America. In: Berryman, A.A. (eds) Dynamics of Forest Insect Populations. Population Ecology. Springer, Boston, MA.

Harvey, B. J., R. A. Andrus, M. A. Battaglia, J. F. Negrón, A. Orrego, and T. T. Veblen. 2021. Droughty times in mesic places: factors associated with forest mortality vary by scale in a temperate subalpine region. Ecosphere 12.

Lalande, B. M., K. Hughes, W. R. Jacobi, W. T. Tinkham, R. Reich, and J. E. Stewart. 2020. Subalpine fir mortality in Colorado is associated with stand density, warming climates and interactions among fungal diseases and the western balsam bark beetle. Forest Ecology and Management 466:118133.

Mitchell, R. G. 1966. Infestation characteristics of the Balsam woolly aphid in the Pacific Northwest. Research Papers. Pacific Northwestern Forest and Range Experiment Station.

Mitchell, R. G., and P. E. Buffam. 2001. Patterns of Long-Term Balsam Woolly Adelgid Infestations and Effects in Oregon and Washington. Western Journal of Applied Forestry 16:121–126.

Smith, J. M., J. Paritsis, T. T. Veblen, and T. B. Chapman. 2015. Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. Forest Ecology and Management 341:8–17.

Zilahi-Balogh, G. M. G., L. M. Humble, R. Foottit, and A. Stock. 2016. History of the balsam woolly adelgid, Adelges piceae (Ratzeburg), in British Columbia, with notes on a recent range expansion. Journal of the Entomological Society of British Columbia 113.

CHAPTER 2

INTERACTIONS BETWEEN HOST TREE AND FOREST CHARACTERISTICS AND THE BALSAM WOOLLY ADELGID IN RECENTLY INVADED AREAS OF NORTHERN UTAH AND SOUTHEASTERN IDAHO

Abstract

The balsam woolly adelgid *Adelges piceae* (Ratz.), BWA, is an invasive forest insect native to central and southern Europe that was first detected in Utah in 2017. It is an obligate, herbivorous parasite of true firs (*Abies* spp.) in both its native and introduced range. It is not a significant pest in its native range in Europe likely due to a long evolutionary relationship with its primary host - *Abies alba* (Mill.), European silver fir. BWA has been identified as the cause of extensive damage in some true fir populations in North America and in North American species planted in Europe (Balch, 1952; Varty, 1956; Skulason et al., 2016). Subalpine fir, *Abies lasiocarpa* [Hook] Nutt., has been identified as the host species most at risk to experience high-intensity damage and mortality (Hain, 1988). With continued range expansion within Utah and potentially into Wyoming, we examined the invasion and life history of the insect in preparation for studying the host-specific, community level, and abiotic characteristics that may influence the observed damage attributed to BWA.

To elucidate the interactions between BWA and its host forests, we collected data on host trees, including size, injury level and BWA-specific symptoms, as well as metrics describing stand characteristics such as structure, density, and composition. Our analysis revealed that the structural complexity of subalpine fir stands was the most crucial stand

characteristic for predicting BWA-related damage. We observed that stands with lower structural complexity experienced more severe damage. Interestingly, we also found evidence suggesting that subalpine fir with symptoms of fir broom rust, *Melampsorella caryophyllacearum* [D.C.] J. Schröt, exhibited lower BWA-specific symptoms. Furthermore, we explored the predictive power of non-climatic abiotic factors and their association with BWA-related damage. Although these results were inconclusive, we theorize that they provide evidence of the temporal history of BWA's invasion into northern Utah. Our study sheds light on the interactions between BWA and subalpine fir stands and contributes to the development of effective management strategies for addressing BWA-induced damage in forest ecosystems within northern Utah and southeastern Idaho.

Introduction

BWA invasion history

Balsam woolly adelgid (BWA) is believed to have been present in North America since at least 1900. It was first detected in Brunswick, Maine in 1908 and was discovered in several locations in southern Nova Scotia, Canada, soon thereafter. By the early 1950s, additional infestations had been discovered in New Hampshire, Vermont, Massachusetts, and New York in the United States and New Brunswick and Quebec in Canada (Balch, 1952). BWA was first detected in Skyland, Virginia in 1956 and on Mt. Mitchell in North Carolina in 1957 on Fraser fir (*Abies fraseri* [Pursh] Poir.) and in other locations across the southern Appalachians soon thereafter (Amman, 1962, 1966). Fraser fir proved to be particularly susceptible to the impacts of BWA, and it was placed on the International

Union for Conservation of Nature's Red List of Threatened Species as "Endangered" in 2011 in part as a response to mass die-off of stands caused by the insect (Farjon et al., 2013).

Along the western coast of North America, BWA was first detected in 1928 at two locations in the San Francisco Bay area: on silver fir, noble fir (*Abies procera* Rehd), blue noble fir (*Abies procera* var. *glauca* [Ravenscr.] Carrière), and grand fir (*A. grandis* [Dougl.] Lindl.) in Golden Gate Park, San Francisco. In the same report, observations on grand fir approximately 23 km to the southeast in Hillsborough, California (Annand, 1928) were also reported. Shortly after 1930, the first accounts of BWA in Oregon were reported in the Willamette Valley with spread through the coastal ranges of noble fir and grand fir (Keen, 1952). Likewise, E. P. Venables and R. Hopping were the first to report the insect in British Columbia in 1937, but efforts to delimit its estimated range did not occur until 1957 (Zilahi-Balogh et al., 2016). By 1956, an estimated 144,000 hectares across Oregon and Washington were infested by BWA, and the insect occurred in the Cascade Mountain Range from Umpqua National Forest in the south to as far as Mt. Baker, Snoqualmie National Forest in northern Washington (Whiteside, 1957). In 1974, BWA was detected in the Blue Mountains of eastern Oregon (Livingston et al., 2000). If an introduction vector was suspected of initial infestations, it was generally attributed to the importation of infested nursery stock from Europe (Balch, 1952; Johnson and Wright, 1957).

In 1983, BWA was reported for the first time in Idaho near Coeur d'Alene on subalpine fir, and to a lesser extent on grand fir (Livingston et al., 2000). New detections were found in the south and west of Idaho before its presence was confirmed in Montana in 2007 and Utah in 2017 (Alston et al., 2018). While suitable habitat exists and BWA infestations are known to occur within 20 km of Wyoming and Colorado, BWA has not yet been confirmed in either state (Davis et al., 2020). It is unknown whether BWA colonized as a “flaming front,” moving more or less linearly in space, from Idaho south through the Bear River Mountains in northern Utah before being detected near Salt Lake City, or if BWA “jumped” from southern Idaho to forests surrounding Salt Lake City before coalescing within the adjacent mountains. The cryptic nature of this insect makes reconstruction of its range expansion difficult at finer resolutions, and questions remain about the patterns of infestation across regional scales.

BWA life history and host feeding

BWA is a member of the Hemipteran family Adelgidae: hemimetabolous relatives of scales and aphids. The family contains 50-70 species in total, a majority of which belong to the *Adelges* or *Pineus* genera. All adelgids are native to the Northern Hemisphere and feed on conifers found in temperate and boreal environments (Havill and Foottit, 2007). BWA is identified as a member of the *Adelges* (*Dreyfusia*) *piceae* species complex along with five currently named subspecies (Havill et al., 2021). The first life stage to hatch from eggs, first instar nymphs, is approximately 0.35-0.40 mm in length, and adults range from 0.65-0.80 mm, however adults can occasionally cross 1 mm in length (Mitchell, 1966; Foottit and Mackauer, 1983; personal observation). There are three recognized geographic subspecies of *Adelges piceae* in North America: *Ad. piceae* [British Columbia, western United States, southeast United States]; *Ad. piceae occidentalis* [British Columbia], and *Ad. piceae canadensis* [Canadian Maritime

Provinces and northeastern United States] which are distinguished by morphology and life cycle characteristics. Phylogenetic studies have identified the populations in Utah and Idaho as members of *Ad. piceae* (Foottit and Mackauer, 1983; Havill et al., 2021).

The life cycle of BWA consists of five life stages: egg, three nymphal instars, and adult. Brood sizes per female are highly variable in the number of eggs laid, ranging from five to fifteen to greater than one or two hundred (Balch, 1952; Amman, 1970). Within our study area, egg mass sizes above thirty are rare (personal observation). Amman (1970) also found that brood size appeared to decrease in conjunction with the age of an infestation and was not strongly correlated with densities of live adelgids which may reach upwards of thirty-one adults per cm^2 of bark surface area (Varty, 1956). Egg incubation time is variable; approximately 12 days (Balch, 1952). Once hatched, 1st instars (often referred to as “crawlers”) will begin to search for a suitable host tree site to insert their stylet. Light intensity, shading, and tree bark cuticle thickness have been shown to influence crawler movement and feeding site selection behavior. Crawlers can move approximately 50 cm/hour and typically settle within 24-48 hours of hatching and in relative proximity to their hatching site if they are not dispersed by wind or fall from the tree (Balch, 1952; Atkins and Hall, 1968; Livingston et al., 2000). Wind is likely the primary mechanism of dispersal for BWA both to new, uninfested stands and within already infested stands (Lass et al., 2014; Rideout et al., 2023). Following settling and stylet insertion, individuals will not relocate and will complete their life cycle in this fixed location.

After the stylet has been inserted, the crawler undergoes morphological changes and darkens in color from rust-red while unsettled to blue-black after settling. Once settled, the nymph begins to exude wool-like wax threads from glands located along each side of the dorsum as it feeds on the host tree's parenchyma tissue (Varty, 1956; Hain, 1988). In this state, 1st instars are believed to enter diapause during the coldest months of winter and aestivate in the warmest months (Amman, 1962), although conditions for diapause induction or maintenance have not been described. In temperate climates, diapause may not occur (Mitchell et al., 1961; Arthur and Hain, 1984). Individuals remain sessile through the 2nd and 3rd instars and continue to grow in size and develop the protective waxy covering that gives them a woolly appearance before completing their final molt. The woolly coverings of adelgids are visible to the naked eye and often referred to as "woollies." Once the adelgid has undergone its final molt to an adult, it begins to lay eggs. Oviposition is estimated to occur for two to greater than five weeks after which the adult dies (Balch, 1952; Mitchell, 1966).

BWA populations in North America follow an anholocyclic lifecycle where reproduction occurs asexually via parthenogenesis on true fir hosts; as such, males are virtually nonexistent in the population at large, and all hatched nymphs are genetic clones of their parent. However, there is some evidence of BWA reproduction occurring via a holocyclic lifecycle - a complex lifecycle that includes both sexual and asexual reproduction and host-switching from true fir hosts to *Picea* spp. hosts; sexual forms have been reported to occur very rarely in North America, and only in Canada's Maritime Provence (Balch, 1952). Havill et al. (2021) found evidence of galls induced by BWA on Caucasian spruce (*Picea orientalis* [L.] Link) and theorized that hybridization with *Adelges nordmannianae* (Eckstein) may enable BWA to potentially complete sexual reproduction in North America, but no direct evidence of such as been found.

Adelgid stylets are approximately four times the length of the body and are capable of extreme maneuverability within the wood of the host. A bead of structural proteins and gel saliva is deposited at the insertion point which will harden as the adelgid probes and is continuously excreted during the initial probing process. This forms a stylet sheath that serves to facilitate penetration and acts as a fulcrum point as the stylet enters and aids in protection from the host immune response (Varty, 1956; Oten, 2012). Adelgids exhibit some measure of control over the stylet's path, and probing behavior has been observed across many species (Dancewicz et al., 2021). The adelgid feeds on parenchyma cells located between the epidermis and phloem and secretes a watery saliva containing digestive compounds to breakdown surrounding starch cells before siphoning the contents into its stylet (Hain, 1988; Havill and Foottit, 2007). The specific chemical makeup of the saliva has not been studied in BWA, but related studies on the hemlock woolly adelgid (*Adelges tsugae* Annand) and other members of Aphidoidea found the presence of trypsin- and amylase-like enzymes that aid in breaking down plant material. Peroxidase and polyphenol oxidase were also found which suggests that the compounds serve a detoxification function (Moreno et al., 2011; Oten, 2012).

BWA hosts

Subalpine fir is BWA's preferred host in the Intermountain region as other available host species are less susceptible. It is a widely distributed, commonly montane species found across western North America from Arizona to Canada's Yukon Territory (Burns and Honkala, 1990). It is the smallest in size of western North America's indigenous *Abies* species. There are two recognized varieties: northern subalpine fir (*A.*

lasiocarpa var. *lasiocarpa* [Hook] Nutt.) and corkbark fir (*A. lasiocarpa* var. *arizonica* [Merriam] Lemmon) which is only found in Arizona, New Mexico, and southern Colorado (Little, 1979). Subalpine fir is found across much of western North America and can occur from near sea level (in southeastern Alaska) to over 3,500 m, though typically occurs between 2,500 to 3,300 m elevation (Alexander et al., 1984). Subalpine fir grows in the coolest and wettest areas of the continental western United States (Thornthwaite, 1948). Temperatures in these areas can vary greatly, ranging from below -45° C in winter to greater than 35° C in summer (Haeffner, 1971; Hanley et al., 1975). It is strongly associated with mixed-conifer forest types but can be found within many other vegetation cover types, particularly in riparian areas.

Within the Intermountain region, subalpine fir is the most abundant true fir and is a key component of one of the region's most important forest cover types, Engelmann spruce (*Picea engelmannii* [Parry] Engelm.)-subalpine fir, or 'spruce-fir.' Engelmann spruce-subalpine fir forests cover approximately four million hectares across the western United States and provide high-value habitat for a variety of native species such as the Rocky Mountain elk (*Cervus canadensis nelsoni* [Erxleben]) and Northern goshawk (*Accipiter gentilis* [L.]). This cover type provides both recreational and commercial uses for communities near and within them (Alexander and Engelby, 1985). Within Utah, the subalpine fir vegetation zone covers approximately 17% of the state's forested area and primarily occurs in the Uinta Mountains and the Wasatch Range while decreasing in abundance along the southern plateaus (Alexander et al., 1984; Graham et al., 1999; Werstak et al., 2016). In these systems, mixed-conifer stands are common. Subalpine fir serves as the late-successional or codominant species with Douglas-fir (*Psuedotsuga* *menziesii* [Mirb.] Franco) and Engelmann spruce, but also commonly occurs as subalpine fir-dominated stands. Typically occurring along the lower elevational range of the Engelmann spruce-subalpine fir cover type, stands of quaking aspen (*Populus tremuloides* [Michx.]) and lodgepole pine (*Pinus contorta* [Dougl.] Loud) will commonly have understories dominated by subalpine fir (Moore, 1964; Eyre, 1980).

The modern structure and composition of many western North America conifer forests differ from the historical condition, contributing to increased insect-caused mortality (Asaro et al., 2023). For example, the early twentieth century coniferous forests of the central Sierra Nevada, California were much less dense and contained trees 50% larger in diameter than modern forests (North et al., 2022). Through settlement-era exploitation and decades of fire suppression, stands with unimodal age class distribution have become more common (Windmuller-Campione et al., 2021). These dense, monotypic stands have several attributes that contribute to increased susceptibility for native and non-native insect infestations. There is evidence that closed canopy structure and reduced tree species diversity (when applicable) can reduce a forest's resilience to severe disturbances including those caused by both native and invasive insect pests (Zhang et al., 2019; Marini et al., 2022). Higher densities of host trees are known to be predictive of greater invasion success – potentially due to increased connectivity of stands (Sharov et al., 1999; Morin et al., 2009). Even-aged stands with little structural complexity (and the management practices that lead to them) can also contribute to the increased presence and damage of insect pests that prefer trees of a particular size (Björkman et al., 2015; Klapwijk et al., 2016).

As a consequence of increasing tree mortality and severe, large-scale mortality events, the fate of western North American forests is of concern. Non-native insects and associated damage can greatly affect forest structure and composition, which in turn can alter ecosystem functioning. This is especially concerning within the context of climate change. Rising regional temperatures have been linked with increases in overall tree mortality across the western United States (van Mantgem et al., 2009; Williams et al., 2013). Insects, both native and invasive, are highly sensitive to temperature. Predicted changes in temperature and seasonal variability across the western United States may result in (and have, in some instances) changes in phenological outcomes of tree-killing insects, including increased voltinism and range expansion and contraction, which can have positive effects on insect population survival (Bale et al., 2002; Berg et al., 2006; Currano et al., 2008; Bentz et al., 2019).

Compared to its common cohorts, there is comparatively little research-based information on the causes and interactions among agents of subalpine fir mortality. Increasing temperatures and reduced precipitation, western balsam bark beetle (*Dryocoetes confuses* [Swaine]), and fungal diseases such as Armillaria root rot (*Armillaria* spp.) have been identified as agents of mortality in subalpine fir (Lalande et al., 2020; Harvey et al., 2021). The widespread increase in subalpine fir mortality is typically described as the "subalpine fir mortality complex" or "subalpine fir decline" — catch-all terms representing the assemblage of potential agents of disturbance and mortality (Table 1). Interactions among BWA and other biotic components of subalpine fir decline are not well understood, but research on balsam fir (*Abies balsamea* [L.] Mill.) suggests that adelgid feeding can be a factor in predisposing hosts to Armillaria root rot infection (Hudak and Singh, 1970). The presence of multi-stressors can drastically alter a forest's canopy structure and composition, and the introduction of a severe invasive pest into these systems could greatly impact the severity and spatial extent of subalpine fir mortality.

Table 1. Insects and pathogens included in the subalpine fir “mortality complex”. Susceptibility refers to the inherent sensitivity of a species to a pest. Vulnerability refers to the potential impact or harm caused by pests once a tree has been affected. Susceptibility and vulnerability rankings are approximate and determined independently of other members of the “mortality complex” (Peterson, 1964; Brooks et al., 1987; McDonald et al., 1987; Hain, 1988; Stock, 1991; Hansen, 1996; Hagle, 2007).

Common name	Species name	Susceptibility	Vulnerability	Symptoms
Insects				
Western balsam bark beetle	*Dryocoetes confusus*	Moderate	High	Galleries, boring dust, pitch tubes
Western spruce budworm	*Choristoneura freemani*	Moderate	Moderate	Defoliated branches, pupae on branches
Balsam woolly adelgid	*Adelges piceae*	Hight	High	Gouting, woollies, crown damage
Fungi				
Armillaria root rot	*Armillaria* spp.	Moderate	Moderate	Clustered, light brown mushrooms White fan-shaped mycelia
Annosus root disease	*Heterobasidion parviporum*	High	High	Little outward symptoms, conks within decayed stumps
Fir broom rust	*Melampsorella*	High	Low	Yellow to light green witch’s brooms

BWA effects

The negative effects of BWA infestation on individual trees can be described in two parts: damage to the bark and sapwood, and damage to the crown and foliage (Hollingsworth and Hain, 1991). When attacked by BWA, the host wood undergoes several structural and chemical changes. Within the live wood, feeding elicits a response by the host's immune system including the release of juvabiones, which have been detected at elevated levels within live wood beneath adelgid feeding sites (Arthur and Hain, 1987). BWA attack induces the production of resin canals and abnormal xylem tissue within the cambium resulting in the creation of rotholz (morphologically similar to compression wood) which greatly impedes the host's ability to move water throughout the stem (Balch et al., 1964; Westing, 1968). Rotholz has been used as a diagnostic symptom of BWA attack in other regions, but in the Intermountain region, it appears to be exceedingly rare and has yet to be documented. BWA attack has been shown to result in a reduction in the water permeability of sapwood and a physiological state similar to drought (Balch, 1952; Puritch, 1971). Adelgid feeding encourages the host tree to increase the production of parenchyma cells which may result in an increase in annual radial growth in the first few years of an infestation and encourages the swelling of the living tissue resulting in shape deformities (i.e., gouting, Schooley and Bryant, 1978).

R.E. Balch was the first to connect the "gout disease" that foresters had noted in Nova Scotia balsam fir stands and the presence of BWA (Balch, 1932). Since then, gouting has become a key diagnostic tool in determining if BWA is or was active in a stand. It typically affects the nodes (terminal nodes, most often) and lenticels of twigs and branches, but severe gouting may be exhibited by swelling throughout a branch (Mitchell, 1966; Amman, 1970). Damage to the crown can manifest in several ways. Deformities from gouting may occur on the leader of trees which may result in the loss of apical dominance (Ragenovich and Mitchell, 2006; personal observation). Over time, the crowns of trees will experience branch flagging and crown dieback (Hain, 1988). Crown flagging and dieback typically increase over time, but it is not uncommon for some individuals to recover. Gouting and stem deformities are unlikely to be repaired unless the tree overgrows the damaged nodes or the tree is relatively young (Balch, 1952; Harris, 1973; Mitchell & Buffam, 2001).

There remains a lack of knowledge in understanding the variation in responses by true firs to BWA attack. Previous studies have illustrated differing levels of resistance to attack among North American true firs. Shasta red fir (*Abies magnifica* var. *shastensis* [Murray bis]), white fir (*Abies concolor* [Gord. & Glend.] Lindl.), and noble fir exhibit much greater resistance to infestation and damage with comparatively little mortality (Mitchell & Buffam, 2001; Overhulser et al., 2004). Subalpine fir and Fraser fir are more susceptible to both infestation and injury relative to other species, with severe mortality occurring in as little as three years (Mitchell et al., 1961; Bryant, 1974; Hain, 1988). In Oregon in the 1950s and 60s, Mitchell described subalpine fir mortality from BWA within abbreviated time frames; however, rapid tree mortality does not always occur.

Within a true fir species, there is also substantial variability in BWA impact. Damage within infested stands can vary dramatically with some trees supporting large populations of BWA and exhibiting severe symptoms of attack while others are unaffected – either by a reduction in injury symptoms (i.e., gouting, crown dieback) or by a lack of detectable infestation (Mitchell, 1966; Harris, 1973; Overhulser et al., 2004).

Host tree size may play a role as greater outer bark thickness is believed to provide resistance from reduced access of the insect's stylet to live wood (Schooley and Bryant, 1978). Bark thickness is influenced by several tree characteristics such as diameter, aspect, and age, but there can be considerable variation among individual trees and locations (Sonmez et al., 2007; Stängle and Dormann, 2017). Furthermore, there are likely to be interactions between biotic and abiotic stand characteristics and BWA infestations. Subalpine fir sites that exhibited greater stem infestations and damage symptoms were associated with higher site quality (high soil productivity, optimal climate conditions) and lower elevations (Mitchell & Buffam, 2001; Overhulser et al., 2004). BWA is often characterized by the mortality it causes and not how it interacts with stand-level characteristics (Hrinkevich et al., 2016). The spread and severity of multiple forest insects can be influenced by stand density, stand structure, and species composition (Björkman et al., 2015; Klapwijk et al., 2016), but there is a lack of knowledge of how these attributes impact BWA.

The recent invasion of BWA into southeastern Idaho and Utah has raised concerns about infestation levels and mortality in subalpine fir stands and generated regional interest in BWA dynamics. However, due to the variability in the distribution and damage of BWA within and across stands of true firs and the lack of established relationships regarding the interaction between BWA and subalpine fir in northern Utah relative to other areas of the Intermountain region, there exists a substantial knowledge gap. Our goal was to describe the relationships between observed BWA damage and characteristics of the host tree, and local stand and abiotic site conditions. Specifically, we examined 1) the relationship between host tree characteristics and BWA-related damage, 2) the importance of stand structure, density, and composition to observed BWA damage, 3) the impact of abiotic factors on BWA severity ratings and subalpine fir mortality, and 4) the interactions among BWA and other subalpine fir pests.

Methods

Study sites

Thirty-nine study sites were identified through coordination with the United States Department of Agriculture (USDA) Forest Service Rocky Mountain Research Station and USDA Forest Health Protection. Potential sites were assessed for both the presence of host trees and for indications of active BWA infestations. Gouting has been used as an indicator of BWA presence in several previous studies (Balch, 1952; Harris, 1973; Quiring et al., 2008) and was our primary method of identifying BWA infestations. However, to confirm that infestations were active, the occurrence of woollies on the bole/branches of host trees within the immediate vicinity of the plot centroid (approximately twenty meters) was the criterion used. Sites were located in northern and northern Utah and southeastern Idaho (Figure 1).

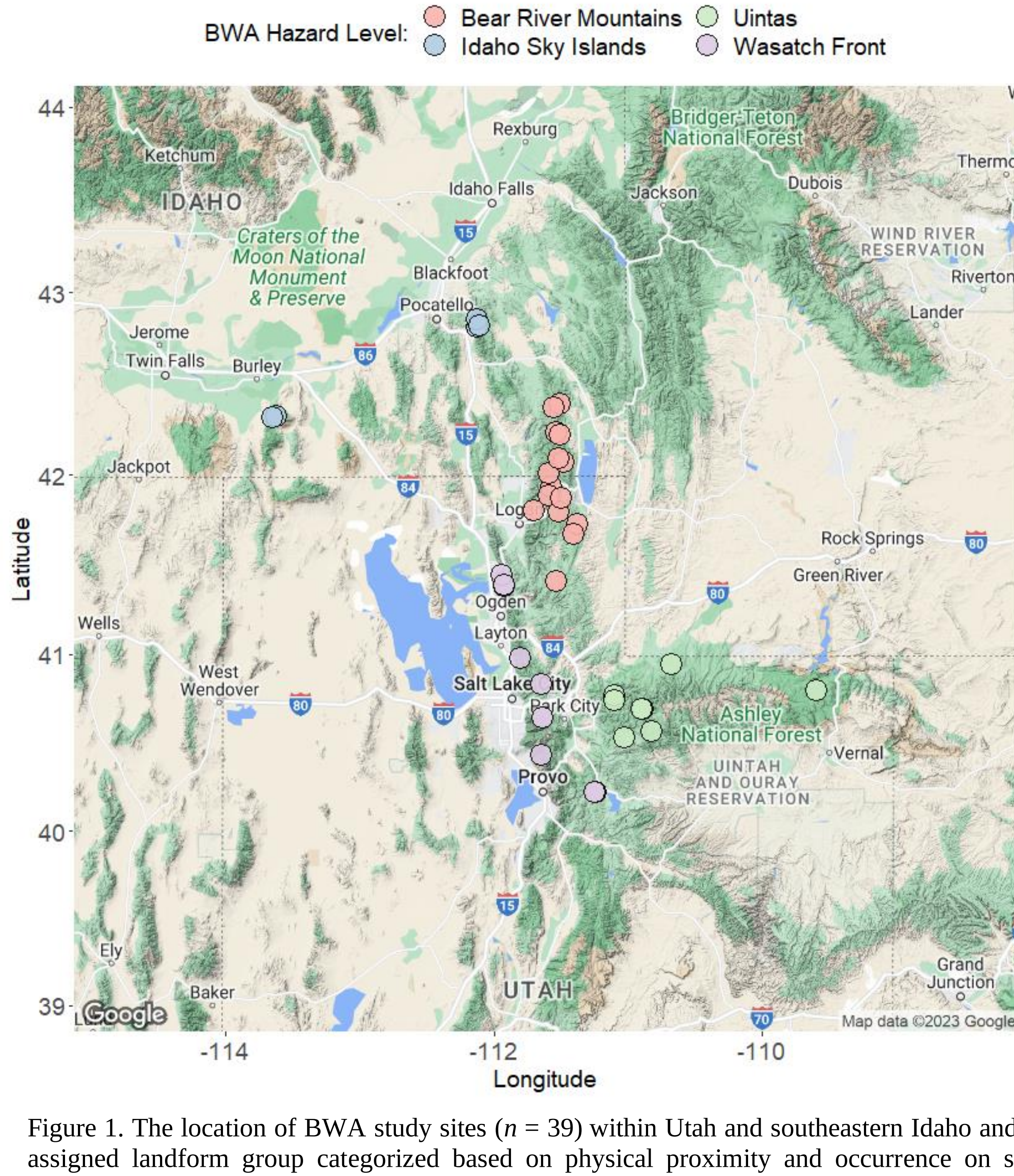

Figure 1. The location of BWA study sites (n = 39) within Utah and southeastern Idaho and their assigned landform group categorized based on physical proximity and occurrence on shared landform(s).

Data collection

When possible, plot establishment occurred through navigation to previously recorded GPS coordinates of BWA infestations. Once within ~3 m of the recorded point, an assessment of BWA infestation occurred. If an active infestation was found, a random azimuth (between 0-360°) and distance (1-10 m) were generated and followed. At that location, the plot was established. Plots were designed as an 11.35 m radius circle (representing 1/250th of a hectare) using a 30 m transect tape to delineate plot radius along cardinal directions. If a plot was co-located with a BWA phenology site established previously (Rideout et al., 2023), the plot center was 2 m directly north from that site. If previously unrecorded infestations were discovered, the first tree displaying identifying symptoms was treated as the GPS point and establishment proceeded as mentioned. Plots were not established if the distance between the perimeters of a proposed plot and any previously established plot would fall within the same hectare.

From the plot center, the following data were recorded: latitude, longitude, aspect of the slope (to the nearest degree), angle of the slope (to the nearest degree), and an overall visual assessment of potential BWA damage following previous rating systems (Bechtold and Patterson, 2005; Hrinkevich et al., 2016; Table 2). Overstory trees (≥ 12.7 cm in diameter at breast height, 1.37 m, DBH) that fell within the plot were sampled and assigned a unique identifying number (1 – nth qualifying tree) beginning with the tree closest to 0° N and moving in a clockwise fashion. If the tree was dead, it was measured for: 1) species, 2) DBH, 3) evidence of BWA, bark beetle, or fungal pathogen infestation (see below). If the tree was alive, the following was recorded: 1) species, 2) DBH, 3) tree height, 4) compacted crown ratio (estimated to the nearest percentage in increments of five), 5) signs/symptoms of bark beetle activity and fungal pathogens. If the examined tree was subalpine fir, then the following additional measurements were also recorded for each vertical third of the crown based on Hawksworth (1977): 1) percent crown dieback (scaled rating), 2) percent branch flagging (scaled rating), 3) witch's broom severity (scaled rating) due to fir broom rust (*Melampsorella caryophyllacearum* [D.C.] Schröt). Gouting severity rating, bole infestation rating at 0 - 0.68 m (low) and 0.68 – 1.37 m (medium) within a 7.62 cm^2 area around the bole across each height range that exhibits the highest severity rating, and any crown deformities were assessed (Table 3). The largest, live host tree from each plot was cored with an increment borer. At plots that were BWA phenology sites, all live host trees within the plot were cored.

Table 2. Rating scale systems for examined damage-related variables assessed on subalpine fir above 12.52 cm DBH. For bole infestations, trees were assessed at two height ranges, 0 - 0.68 m (Low – L) and 0.68 – 1.37 m (Medium – M). Bark beetle refers to the western balsam bark beetle, *Dryocoetes confuses*.

	Crown Dieback	Branch Flagging	Bole Infestation at L/M	Gouting	Fir Broom Rust	Bark Beetle	Fungal Pathogen
Scale:	0-5	0-5	0-4	0-3	0-3	0-1	0-1
0	0%	0%	Undetectable	Undetectable	Undetectable	Undetectable	Undetectable
1	1-24%	1-24%	1-5%	Light swelling, indistinct without close examination.	Present on 1-19% of branches.	Signs of bark beetle detected.	Signs of root rot or fungal infestation observed.
2	25-49%	25-49%	6-19%	Moderate swelling, distinct on bare and foliated branch tips.	Present on 20-49% of branches.		
3	50-74%	50-74%	20-49%	Severe swelling, distinct and prominent branch distortion.	Present on ≥50% of branches.		
4	75-99%	75-99%	≥ 50 %				
5	100%	100%					

Table 3. Definitions of terms referenced in field sampling methodology.

Terms:	Definitions**:**
Site	The overarching geographic area that may host one or more BWA infestations and is homogenous in terms of physical and biological environment (Skovsgaard and Vanclay, 2008). Sites will be given a unique four-letter code to differentiate them (i.e., Farmington Canyon -> FARM).
Plot	The spatial area in which measurements of variables of interest are collected. Each plot is located within a site and is given a unique two-number identifier (i.e., FARM01, FARM02).
Vertical 1/3rd	One-third of the vertical length of the crown – composed of "Top," "Middle," and "Bottom." Each *Abies* over 2.54 cm DBH will have a measurement for the following variables recorded for each vertical 1/3rd: Crown Dieback, Branch Flagging, Parasite Complex. Design from Hawksworth, 1977.
Compacted Crown Ratio	The proportion of total tree length that supports live foliage; a visual estimate that substituting empty areas of the crown with foliated areas that occur on lower sections (Bechtold and Patterson, 2005; Toney and Reaves, 2009).
Crown Dieback	Recent mortality in the crown showing foliage loss along branches with twigs that begins at the terminal portion of a branch and continues toward the trunk; an example of the process can be found in Figure 3 (Schomaker et al., 2007).
Branch Flagging	Assessment of the percentage of needles that have become discolored or dead but remain attached to the branches. Flagging that is the result of a mechanical injury is not included in the estimate.
Fir Broom Rust	Epicormic growth resulting in brooms created by fir broom rust (*Melampsorella caryophyllacearum*). Assessed on symptoms listed in Hagle et al., 2003.
Gouting	Visual estimate of the mean level of gouting visible among the terminal portion of branches in the crown.
Bark Beetle	Trees will be assessed on the presence/absence of signs and symptoms associated with Scolytinae. Visual identification, exit holes, resin flow, frass or boring dust, and galleries (Hagle et al., 2003).
Fungal Pathogen	Trees expressing symptoms of root disease are assessed on the presence/absence of external symptoms associated with root rot diseases; when possible, bark will be separated from the wood to check for mycelium fans (Hagle et al., 2003).

Analytical approach

Host tree characteristics and BWA infestation

To develop a simplified index describing crown damage, we averaged crown dieback and flagging across vertical thirds and divided by five (the maximum rating possible) to create an index scaled to 0 – 1. These were then averaged to create a single 0-1 index describing crown damage (CDAM). As no widely accepted metric exists for assessing BWA damage to individual trees, we examined three metrics: crown damage (CDAM), crown damage and gouting (CDG), and BWA-specific symptoms, gouting and mean bole infestation across low and medium heights. (SYMP) (Table 4).

Table 4: Formulas for the metrics used to estimate BWA-related damage on individual trees and the basal area scaler used to adjust BWA-related damage to aboveground biomass.

Metric	Formula
Crown Damage (CDAM)	$CDAM = \frac{\left(\frac{Dieback}{5}\right) + \left(\frac{Flagging}{5}\right)}{2}$
Crown Damage with Gouting (CDG)	$CDG = \frac{\left(\frac{Dieback}{5}\right) + \left(\frac{Flagging}{5}\right) + \left(\frac{Gouting}{3}\right)}{3}$
BWA-specific Symptoms (SYMP)	$SYMP = \frac{\left(\frac{Gouting}{3}\right) + \left(\frac{mean(Bole\ Infestation)}{4}\right)}{2}$
Basal Area Scaling for Plot Level	For tree$_j$ on plot$_i$: $CDAM, CDG, SYMP \times \frac{Basal\ Area_{ji}}{\max(Basal\ Area_i)}$

To assess relationships between host tree level characteristics and BWA infestations, we used Welch's two-sample t-tests and one-way ANOVA when appropriate. When ANOVAs indicated a variable was significantly different, Tukey HSD tests were conducted. In identifying the contribution of host tree-level variables to the impact of BWA, we used linear multiple regression with CDG and SYMP as the response terms. Independent variables were selected by dividing variables into a priori groups based on shared characteristics (i.e., host tree size or presence/absence of other pests) and a correlation matrix was constructed to eliminate variables that covaried. After these models were run, variable inflation factors (VIF) were calculated, and any variables that were above 5.0 were removed in a stepwise approach. This process was repeated until no predictor variable had a VIF score above 5.0.

Stand characteristics and BWA infestation

For characterizing stand density and stocking, we calculated basal area per hectare (BA), trees per hectare (TPH), Reineke's stand density index (SDI_R), additive stand density index (SDI_Σ), and relative SDI. To characterize stand structure, we calculated quadratic mean diameter (QMD) and the SDI ratio (a plot's SDI_R divided by its SDI_Σ) for both host trees and all trees. Stand composition was described by calculating the percentage of basal area of a plot that belongs to the host species (BA%). The percentages of trees on the plot that were affected by BWA bole infestations, bark beetle, fir broom rust, and fungal pathogens were also calculated. Because the largest trees comprised a majority of the stand's aboveground biomass and are therefore more important than smaller members of the stand, we scaled the BWA severity metrics by individual-tree BA (Lutz et al., 2018; Table 4).

To identify relationships between stand-level characteristics and BWA-related damage, we used linear multiple regression. We selected CDG as our primary response variable at the stand level because it characterized crown damage (the clearest indicator of tree stress) and because the inclusion of gouting helped to separate the impact of BWA from other causes of crown damage. We applied a natural log transformation to scaled CDG to meet assumptions of normality and homoscedasticity and tested groups of predictor variables based on their shared qualities, i.e., non-climatic abiotic factors or host-specific metrics. From these regressions, we constructed a composite model which included the best preforming variables across groups. Our best-performing, stand-level linear model was then used in the construction of a mixed-effect model with scaled CDG as the response variable using the “lme4” package (v1.1.30; Bates et al., 2015) in R 4.2.1 (R Core Team, 2022). Plots were categorized into five “landform groups” according to shared landform(s) (Figure 1). These landform groups were subsequently assigned a random effect in the mixed-effect model. Furthermore, we conducted one-way ANOVA tests to examine significant differences in the means of damage metrics among these groups, and when necessary, we performed Tukey HSD tests.

Abiotic factors and BWA infestation

The impact of abiotic factors on host-level damage was evaluated using linear mixed-effect models with plot ID serving as the single abiotic term and assigned as the random effect. A linear regression model was constructed to investigate how abiotic factors affected scaled, stand-level damage with CDG as the response variable. Fixed effects were assigned to the best-performing predictor variables from the linear multiple regression models. Plot ID was included as a random effect to represent the variation among trees at different plots. The model was constructed using the “lme4” package.

As plots occurred across a representative elevational gradient of subalpine fir presence, we specifically examined the relationships between elevation and stand-level metrics of BWA damage using linear regression. In doing so, we chose to examine both the scaled and unscaled metrics of BWA damage, CDG, and SYMP.

Co-morbidity agents and BWA infestation

The interplay among BWA and other contributors to the subalpine fir mortality complex was examined using Welch's two-sample t-tests on the presence or absence of bark beetle, fungal disease, and fir broom rust. Due to the small number of live host trees exhibiting signs of bark beetle attack (i.e., frass, pitch tubes, and clear galleries), interactions with BWA were examined at stand-level. Determination of the presence of bark beetles at the stand level used the presence of previously mentioned symptoms and considered live and dead host trees. Additionally, a one-way ANOVA was run for the maximum severity rating for fir broom rust across vertical thirds of the crown with mean bole infestation rating and gouting rating as response terms. Linear multiple regression was also used to elucidate the relationship between agents of co-morbidity (bark beetle and fungal disease presence or absence, mean fir broom rust rating) and their impact (CDAM) on BWA-specific symptoms (mean bole infestation, gouting rating, and SYMP).

Results

Host tree characteristics and BWA infestation

Of the 505 overstory subalpine fir assessed for BWA-related symptoms and damage, a total of 470 (93.1%) exhibited either gouting or bole infestations (Table 5). On the 0 – 5 rating scale, total combined crown damage (CDAM) was 1.29 ± 0.03 across all subalpine fir. The mean bole infestation density was 0.61 ± 0.03 on a 0 – 4 scale. Forty-two of the 316 trees with woollies on the bole had infestation ratings higher than 1 (>5% of the observed area covered in woollies) on either of the two areas of the bole examined. Mean gouting was light at 1.12 ± 0.03. A total of 108 trees had gouting ratings of moderate to severe (2 – 3) with only eight trees being rated as severe. Crown deformities occurred in 26.9% of trees. The linear multiple regression model for CDG using host-level characteristics was significant ($p < 0.01$) but exhibited low goodness of fit (adj. R^2 = 0.20). All input variables were significant. With SYMP as the response term, host variables in the model were not predictive ($p = 0.66$), and no individual input variable was significant.

Table 5: Summary statistics, i.e., mean, standard error of the mean (SE), and scale used, of individual host tree-level damage metrics used in assessing relationships between BWA infestation and host characteristics (n = 505).

Metric		Scale	Mean ± SE
Crown Dieback			
	Top 1/3rd	0-5	0.60 ± 0.04
	Middle 1/3rd		1.38 ± 0.04
	Bottom 1/3rd		2.34 ± 0.05
	Total		1.44 ± 0.03
Flagging			
	Top 1/3rd	0-5	0.68 ± 0.04
	Middle 1/3rd		1.16 ± 0.03
	Bottom 1/3rd		1.56 ± 0.05
	Total		1.13 ± 0.03
Crown Damage			
	Top 1/3rd	0-5	0.64 ± 0.03
	Middle 1/3rd		1.27 ± 0.03
	Bottom 1/3rd		1.95 ± 0.04
	Total		1.29 ± 0.03
Bole Infestation			
	Low (0-0.68 m)	0-4	0.67 ± 0.03
	Medium (0.68-1.37 m)		0.55 ± 0.03
	Combined		0.61 ± 0.03
	Maximum		0.76 ± 0.03
Gouting		0-3	1.12 ± 0.03

From Welch's two sample T-tests, crown damage was not significantly affected by bole infestation presence ($p = 0.29$) but observed gouting was more severe on trees with more severe bole infestation ($p < 0.01$). Crown damage was significantly higher on trees where deformities (abnormalities in a tree's growth form that occur at the top of the crown) were noted (Table 6). The results of the Tukey HSD tests revealed statistically significant differences in the means of crown damage and bole infestation based on the tree gouting ratings. Specifically, the expected values of CDAM were found to be significantly greater on trees with higher gouting ratings ($p = 0.04$). Similarly, the expected values of bole infestation presence were also significantly greater on trees with higher gouting ratings (p < 0.01).

Table 6: Summary of Welch's two sample t-test testing for the effects of individual host tree characteristics on the presence or absence of crown deformity and bole infestation.

	Deformity Present (*n* = 136)	Deformity Absent (*n* = 369)	
	Mean ± SE	Mean ± SE	*P*-value
DBH	30.4 ± 1.02	25.7 ± 0.60	< 0.001
Height	17.3 ± 0.57	15.6 ± 0.30	0.009
Compacted Crown Ratio	65% ± 1.90	67% ± 1.15	0.43
Crown Damage (CDAM)	1.42 ± 0.05	1.23 ± 0.03	0.002
Gouting Rating	1.32 ± 0.05	1.04 ± 0.03	< 0.001
	Bole Infestation Present (*n* = 316)	**Bole Infestation Absent (*n* = 189)**	
	Mean ± SE	Mean ± SE	*P*-value
DBH	26.7 ± 0.66	27.5 ± 0.89	0.46
Height	16.2 ± 0.35	15.7 ± 0.42	0.40
Compacted Crown Ratio	65% ± 1.24	68% ± 1.61	0.03
Crown Damage (CDAM)	1.30 ± 0.03	1.25 ± 0.04	0.29
Gouting Rating	1.18 ± 0.03	1.01 ± 0.05	< 0.01

In the host-level mixed-effect model with plot ID as a random effect, all predictor variables and the intercept were significant (p < 0.01) for CDG. The two terms with the largest standardized coefficients were compacted crown ratio (-0.45) and mean bole infestation (0.18), and the conditional R^2 rose to 0.50 from a marginal R^2 of 0.23 (Table 7). In the mixed-effect model for SYMP, no fixed effect variable was statistically significant (p > 0.5). The marginal R^2 was extremely low (< 0.001) and rose significantly to a conditional R^2 of 0.42.

Table 7: The results of mixed-effect models examining the association between host tree-level characteristics and BWA-related damage (CDG) and symptoms (SYMP). The CDG model focused on BWA-related damage and included the following predictors: DBH (diameter at breast height), mean bole infestation, and compacted crown ratio. The model revealed a statistically significant relationship between the predictors and BWA-related damage, but at low power. The SYMP model examined the association between host-level characteristics and BWA-specific symptoms. The predictors in this model were DBH, CDAM (crown damage), and mean fir broom rust rating.

CDG Model

Parameter	Coefficient	95% CI	*T*(570)	*P*-value
Fixed Effects				
Intercept	0.08	(-0.11, 0.26)	20.22	< .001
DBH	0.11	(0.04, 0.19)	2.90	0.004
Mean Bole Infestation	0.18	(0.09, 0.18)	3.75	< .001
Compacted Crown Ratio	-0.45	(-0.53, -0.37)	-11.14	< .001
Random Effects	Variance			
Plot ID	0.06			
Residual	0.08			
		Marginal $R^2 = 0.23$		Conditional $R^2 = 0.50$

SYMP Model

Parameter	Coefficient	95% CI	*T*(570)	*P*-value
Fixed Effects				
Intercept	0.04	(-0.18, 0.27)	10.20	< 0.001
Mean Broom Rating	0.02	(-0.07, 0.11)	0.41	0.683
CDAM	0.06	(-0.02, 0.14)	1.53	0.125
DBH	0.02	(-0.06, 0.10)	0.41	0.682
Random Effects	Variance			
Plot ID	0.09			
Residual	0.11			
		Marginal $R^2 < 0.001$		Conditional $R^2 = 0.42$

Stand characteristics and BWA infestation

At the stand level (all measured trees ≥ 12.52 cm DBH across thirty-nine plots), mean crown damage was 1.32 ± 0.06 with mean crown dieback and mean flagging at 1.47 and 1.17, respectively. The average percentage of subalpine fir with bole infestations in the overstory was 63.8% ± 0.05, and the range of this value among plots was 0 – 100%. The mean infestation rating was greater on the lower half of the observed bole area compared to the upper half (a mean rating of 0.70 to 0.53 on a 0 – 4 scale), and the combined infestation rating mean was 0.61 ± 0.08 with a range of 0.0 – 2.31. On a 0-3 scale, gouting at the plot level averaged 1.16 ± 0.07 with a range from 0.33 – 2.25. Two plots had mean gouting ratings at or above the moderate rating (≥ 2). Mean scaled CDAM was 0.18 ± 0.01, the highest average across the damage metrics. Scaled CDG and SYMP had means of 0.13 ± 0.01 and 0.12 ± 0.01, respectively. No plot rated higher than 0.50 on any damage metric, and both CDG and SYMP rated no higher than 0.26 on a 0-1 rating. Several metrics that characterized stand structure, density, and composition were calculated as well (Table 8).

Table 8: Summary statistics, i.e., mean, standard error of the mean (SE), and the range of values, of forest structure metrics used in assessing relationships between BWA infestation and stand characteristics. Additional non-climatic abiotic factors are summarized below.

Metric		Mean ± SE	Range
Reineke's Stand Density Index			
	Host	170 ± 15.7	25 — 496
	Total	220 ± 17.9	25 — 588
Summed Stand Density Index			
	Host	159 ± 14.9	24 — 469
	Total	210 ± 17.0	24 — 555
Stand Density Index Ratio			
	Host	0.96 ± 0.003	0.93 — 0.99
	Total	0.96 ± 0.003	0.89 — 0.99
Quadratic Mean Diameter (cm)			
	Host	29.0 ± 1.1	16.0 — 45.8
	Total	30.7 ± 1.2	18.6 — 53.8
	Host-Total Ratio	0.95 ± 0.01	0.64 —1.08
Basal Area (m^3/ha)			
	Host	22.5 ± 2.4	3.0 — 73.5
	Total	30.3 ± 2.8	3.0 — 89.1
	Host-Total Percentage	76.2 % ± 0.04	17.3 — 100 %
Trees per Hectare			
	Host	324 ± 23.0	74 — 717
	Total	404 ± 28.6	74 — 890
	Host-Total Percentage	82.7 % ± 0.03	33.3 — 100 %
Topographic			
	Elevation (m)	2374 m ± 55.8	1816 – 3210 m
	Slope	22.72 % ± 1.85	2 — 54 %
	Folded aspect	60.4° ± 8.36	1 — 177°

The best-performing model included scaled CDG as the response term with host SDI ratio, relative SDI, host QMD, and latitude as input variables (F = 21.84, $p < 0.01$, adj. R^2 =0.69, Table 9). Host SDI ratio was the variable with the largest coefficient by a substantial margin (16.10 – 9.40 for total SDI ratio).

Table 9: The results of two linear models fitted to predict BWA-related damage (scaled CDG) using host QMD, host SDI ratio, relative SDI, latitude, and landform groups. In the composite linear model, the predictors collectively explain a statistically significant proportion of variance (adj. $R^2 = 0.69$, $p < .001$). In the linear mixed-effect model, host QMD, host SDI ratio, relative SDI were considered, with landform group included as a random effect. Latitude's inclusion in the model resulted in a singular fit and was thus excluded.

Composite Model

Parameter	Coefficient	95% CI	T_{34}	*P*-value
Intercept	-14.57	(-21.86, -7.29)	-4.07	< 0.001
Host SDI Ratio	15.64	(11.13, 20.15)	7.05	< 0.001
Host QMD	0.09	(0.06, 0.13)	4.98	< 0.001
Relative SDI	-1.12	(-1.63, -0.62)	-4.53	< 0.001
Latitude	-0.08	(-0.18, 0.03)	-1.54	0.133
		$F_{4, 34} = 21.84$	Adj. $R^2 = 0.69$	$P < 0.001$

Mixed-effect Model

Parameter	Coefficient	95% CI	T_{33}	*P*-value
<u>Fixed Effects</u>				
Intercept	-17.93	(-22.23, -13.64)	-8.49	< 0.001
Host SDI Ratio	15.77	(11.48, 20.06)	7.49	< 0.001
Host QMD	0.09	(0.05, 0.13)	4.45	< 0.001
Relative SDI	-1.08	(-1.59, -0.58)	-4.40	< 0.001
<u>Random Effects</u>				
Landform Group	0.09			
Residual	0.22			
		Marginal $R^2 = 0.63$		Conditional $R^2 = 0.68$

Abiotic factors and BWA infestation

The linear regression model with abiotic factors was nearly significant at 95% confidence ($p = 0.051$). Latitude was a significant predictor of CDG and was included in the composite model (Table 9). From this composite model, we added a random slope effect to the plots' landform group (Figure 1). This mixed-effect model resulted in a singular fit, and we chose to remove the least significant term by p-value (latitude). Removal of this term allowed the model to run successfully. All fixed effect variables and the fixed intercept were statistically significant and estimated coefficients were similar to the linear fixed-effect model (Table 9). Host SDI ratio remained the most important term. Significant differences between the means of CDG were detected for landform group ($p < 0.01$) (Figure 2).

Elevation was a statistically significant predictor of mean bole infestation severity, the percentage of trees with bole infestations, and the occurrence of crown deformities at the stand level ($p \leq 0.05$), but the predictor power of these relationships was minor with adj. R^2 values of 0.17, 0.23, and 0.08, respectively. Mean gouting was not significant at 95% confidence ($p = 0.10$). Elevation was not statistically significant in predicting mortality (as a percentage of host BA). When scaled damage metrics were used as the response terms (CDAM, CDG, and SYMP), there was no statistically significant relationship detected ($p \geq 0.47$).

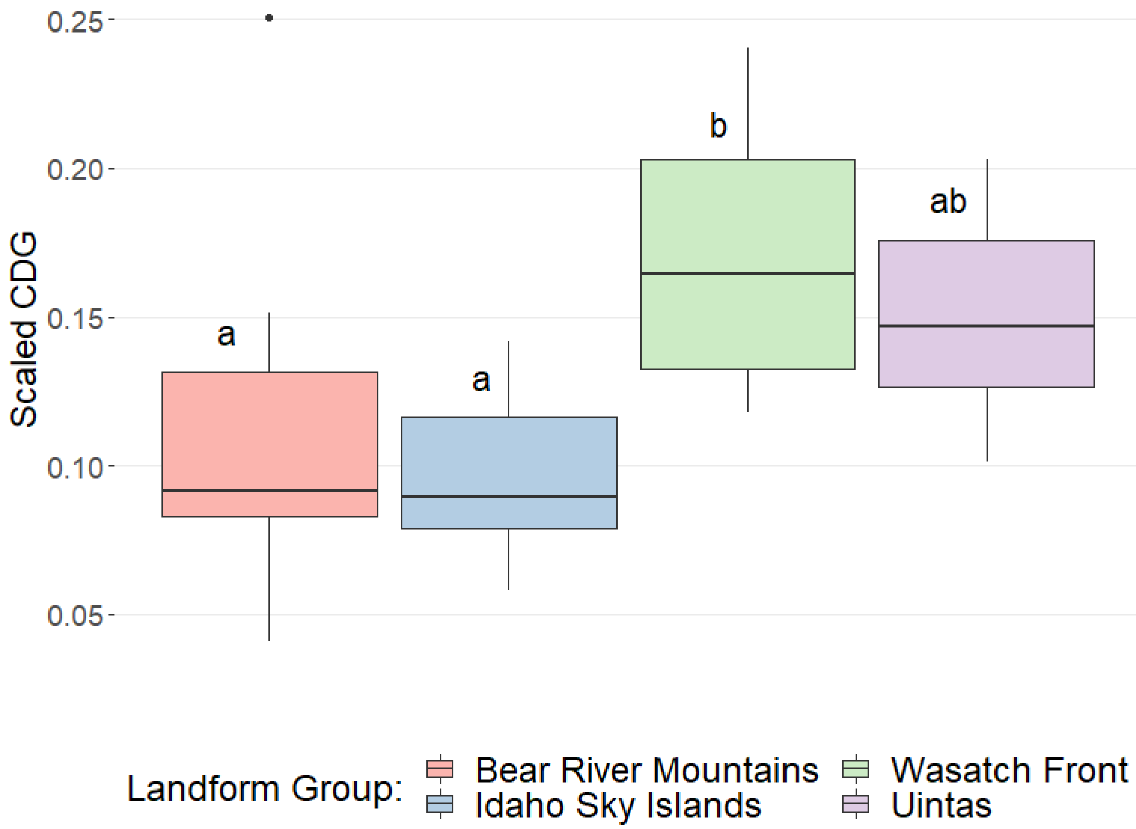

Figure 2: Box and whisker plot examining the mean scaled CDG from plots within differing landform groups. Significant differences in scaled CDG among landform groups are indicated by different letters above the boxplot.

Co-morbidity agents and mortality

Out of a total of 1,534 trees measured, only 175 were classified as dead, resulting in an overall mortality rate of 11.4%. Subalpine fir had the highest incidence of overstory mortality (n = 87) accounting for 73.7% of dead overstory trees. At the stand level, mortality of subalpine fir was only detected at 56% of plots. Across all plots, mean mortality of subalpine fir basal area was 10.6% ± 0.03. At the 22 plots where mortality was detected, the mean was 18.7% ± 0.04. Linear regression and graphic analysis revealed no relationship between stand mortality and stand-level characteristics or abiotic factors.

All measured agents of co-morbidity occurred with high variability (Table 10). On a 0-3 scale, the mean severity of fir broom rust across all trees at the plot level was 0.34 ± 0.06 and a range from 0.00 to 1.31. The mean Gini coefficient for fir broom rust severity was 0.69 ± 0.05. At 14 of 39 plots, symptoms of *Dryocoetes confuses* were detected in dead subalpine fir. Above ground symptoms of fungal disease were an uncommon occurrence with a mean percentage of symptomatic trees of 5.7% ± 0.01. While some plots were recorded with symptomatic rates above 25% of measured trees (range: 0 – 31.3%), the overwhelming majority of detections were of grey-brown saprot, *Cryptoporus volvatus* [Peck] Shear.

Table 10: Host-level summary statistics for fir broom rust severity and above ground fungal disease symptoms. Plot-level summary statistics for the presence/absence of bark beetle symptoms. Fir broom rust severity was assessed by dividing the crown into vertical thirds and recording measurements for each section.

Metric	Scale	Mean ± SE
Broom Severity	0-3	
Top Vertical Third		0.13 ± 0.02
Middle Vertical Third		0.35 ± 0.03
Bottom Vertical Third		0.46 ± 0.04
Combined Crown Rating		0.31 ± 0.02
Maximum Crown Rating		0.63 ± 0.04
Bark Beetle Symptoms	0-1	
Percent of Plots Infested		35.9 %
Fungal Disease Symptoms	0-1	
Percent Infested		5.95 %

We did not find any significant differences in the values of host QMD, CDAM, SYMP, or CDG based on the presence or absence of bark beetle symptoms via Welch's two-sample t-test. The lowest p-value among response terms was 0.18 (belonging to SYMP). Mean bole infestation was significantly higher on trees with presence of above ground fungal disease symptoms ($p < 0.01$). Host DBH and height both failed to reach p-values below 0.05 in differences in the mean values based on the presence or absence of above ground fungal disease symptoms with p-values of 0.06 and 0.12, respectively. Gouting and crown damage were not significant in predicting the presence of above ground fungal disease symptoms.

DBH was not significant in predicting the presence of fir broom rust, but host height was with larger trees being more likely to have fir broom rust. Mean gouting rating ($p < 0.01$, $T = -3.93$) and mean bole infestation ($p = 0.02$, $T = -2.35$), however, were both significantly lower on trees where fir broom rust was present. Crown damage had no meaningful relationship with the presence of fir broom rust or the maximum fir broom rust rating (the highest rating on the 0-3 scale across the vertical thirds of a host's crown) with p-values of 0.98 and 0.39, respectively. Maximum broom rating, however, was significantly higher on trees with less severe gouting ($p < 0.01$) and nearly significant with less severe bole infestation ($p = 0.07$). Considering the SYMP metric (gouting and bole infestation), there were significant differences between groups regarding broom presence/absence and maximum broom rating ($p < 0.01$) (Figure 3).

Linear models examining BWA-related damage (CDG) and BWA-specific symptoms (SYMP) with the presence and severity of biotic agents were statistically significant ($p < 0.01$) but low power (adj. $R^2 \leq 0.01$). Mean fir broom rust was negatively related to SYMP ($p \leq 0.01$). Other explanatory variables (i.e., above ground fungal disease presence/absence, crown damage) were either less or not significant. CDG was not explained by the presence of any other biotic agents.

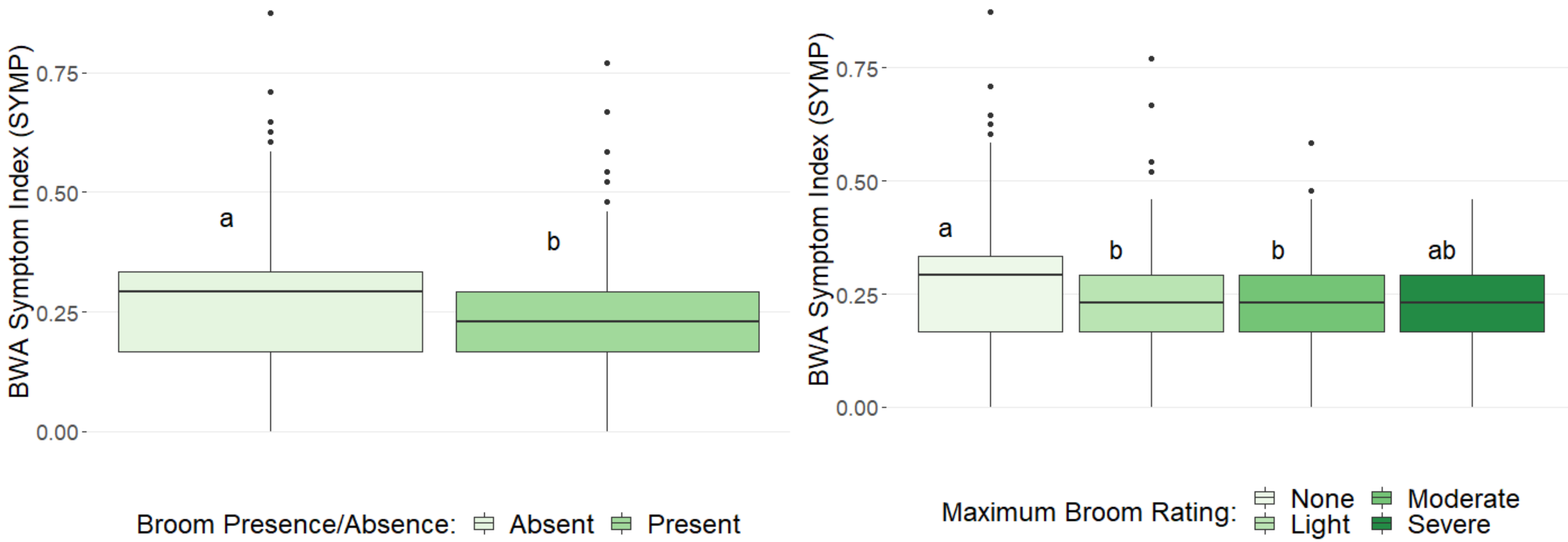

Figure 3: Box and whisker plots illustrating the significant differences among host tree groups based on Tukey HSD tests. Plot 1 (left) displays the significant difference in the mean of BWA-specific symptoms (SYMP) based on the presence or absence of fir broom rust on the host tree. Plot 2 (right) displays the significant differences in mean SYMP among groups of host trees based on the maximum severity rating of fir broom rust on host trees. Significant differences among groups are denoted by letters above the box and whisker plots.

Discussion

Host tree characteristics and BWA infestation

A large percentage (93.1%) of subalpine fir in our plots had BWA-related symptoms of gouting and bole infestation. Gouting, while not commonly severe, was nearly ubiquitous across trees in our study (88.9% of hosts). Others have reported that gouting is the primary identifier for BWA presence, and the percentage of trees with gouting at our plots was substantially higher than was reported in the Pacific Northwest (Overhulser et al., 2004). Bole infestations were more frequent and denser on the lower portion of boles than on the middle which may be due to higher overwintering survival rates for adelgids that occur below the snow line surrounding the bole than adelgids that are more exposed to cold temperatures (Balch, 1952; Schooley and Bryant, 1976). Mean infestation density of the two bole sample areas was low, just below 1-5% of the total bole area. Hrinkevich et al. (2016) noted the importance of crown deformities in estimating BWA impact on stands, and our findings generally agree. Mean values for gouting and bole infestations were higher on trees with crown deformities present. The presence of crown deformities was also highly correlated with crown damage — particularly with damage in the top vertical third of the affected tree's crown. Individual tree characteristics such as DBH and height were often significant. However, they did a poor job of explaining the presence or severity of BWA-related crown symptoms and damage. Studies that examined BWA infestations of balsam fir in Newfoundland suggest that older, larger trees were more likely to host severe infestations and suffer worse damage than smaller, immature trees (Page, 1973; Schooley and Bryant, 1976). We observed that crown deformities were more likely to occur on larger trees, but this did not hold for other symptoms when considering tree size. Nor were any of our damage metrics (CDAM, CDG, SYMP) substantially affected by or predictive of tree size. The Newfoundland studies considered trees below our minimum diameter of 12.52 cm, and they, among others, note that immature trees appear more resilient to BWA-related damage and more capable of rebounding from BWA attack (Balch, 1952; Mitchell, 1966).

Stand characteristics and BWA infestation

To better understand the dynamics between stand-level characteristics and effects on BWA infestations and damage, CDG was scaled by basal area, therefore providing a better representation of BWA impact on aboveground biomass as the largest trees encompass a majority of a stand's biomass. Variables describing host tree characteristics in a stand (e.g., host SDI ratio, host QMD, host TPH) were better predictors of scaled CDG than variables that included all trees species in the stand. This is not surprising given that BWA only attacks and feeds on true fir hosts. Stand structure variables were also more important than abiotic factors in predicting CDG. In particular, host SDI ratio and the SDI ratio of all trees explained more variability in scaled CDG than any other tested variable with large, negatively correlated coefficients. SDI ratio describes the structural variability of a stand where values closer to 1.00 indicate that trees are more closely related in size (and putatively age) to each other, and therefore the overall stand is less structurally complex. We found that stands with higher SDI ratios, and less structural complexity, were associated with greater BWA-related damage. In contrast, structurally complex stands, where a majority of trees fall outside of one standard deviation of the mean DBH, were associated with less BWA-related damage (Figure 4). Structurally simple stands with similar tree sizes and canopy heights may enable inter-canopy spread of BWA to occur more frequently or with greater success. These stand types may also be associated with interspecific competition a potentially compounding factor to increased BWA-related damage. As similarly sized trees compete for light, nutrients, and water, they are less resilient to BWA attack and respond with less efficacy than uneven-aged stands dominated by a few, large hosts that are generally not competing with each other.

Stands with a higher number of host trees and that were also denser overall tended to have less average BWA damage. This seems counterintuitive, but there may be several

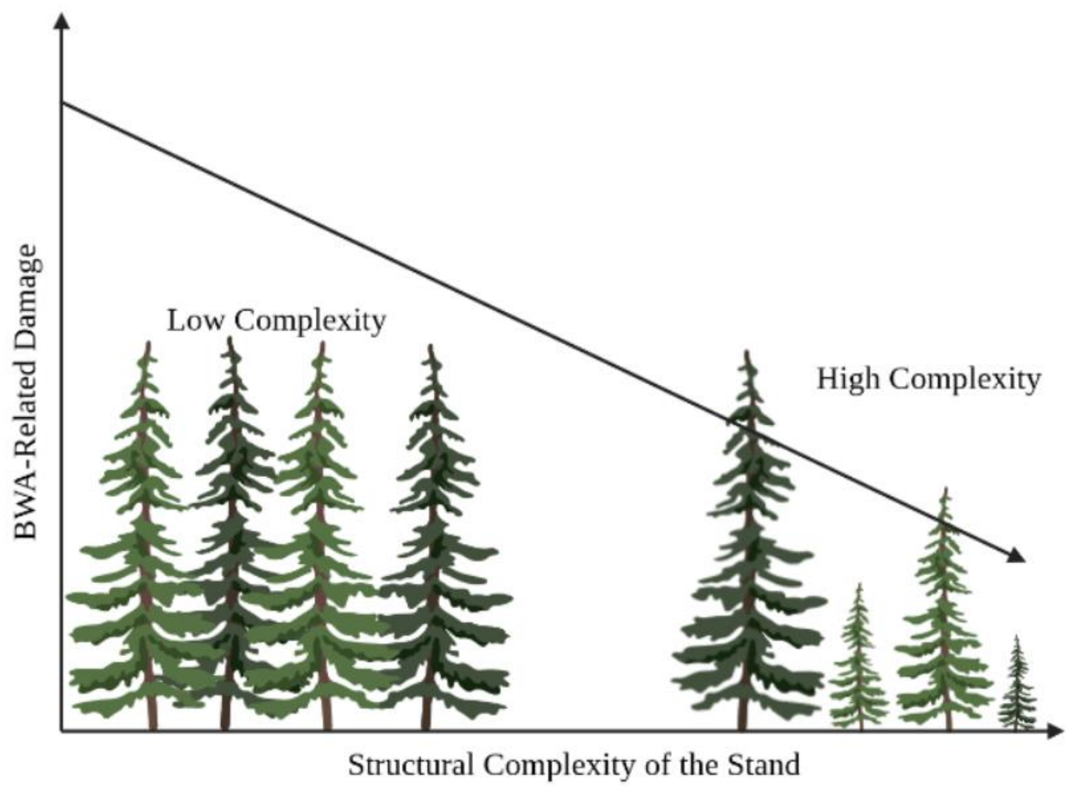

Figure 4: Visualization of the relationship between BWA-related damage and the structural complexity of host trees within stands. Low structural complexity (left) increases the BWA-related damage observed (regardless of the size of the trees). As structural complexity increases, stands are less likely to exhibit severe BWA-related damage (right). Graphic created in BioRender.com.

explanations. Dense stands may be cooler than less dense stands due to canopy closure and have differences in light levels, potentially resulting in less BWA-related damage despite a high number of host trees. Likewise, there may be unmeasured patterns of patchiness that occur in more dense stands that are not present in stands with fewer host trees. This result may also allude to the effects of edge dynamics from which BWA has a more visible impact on trees along the perimeter of a stand (typically, less dense than further into a stand). If BWA is more likely to colonize trees along the edge first before colonizing trees deeper into the stand, then this relationship may be a result of temporal differences in the length of infestation that create this minor effect.

Abiotic factors and BWA infestation

Our study plots covered a broad elevational range, although the majority occurred between 2,000 – 2,500 m, likely due to host availability and site selection. Elevation serves as a proxy for a climate gradient across our plots and was significant in describing BWA-specific symptoms. We found no significant correlation between elevation and stand-level metrics CDAM, CDG, and SYMP or with crown damage — scaled or unscaled. The results for bole infestation and crown damage are unsurprising and corroborate previous research showing that BWA severity is less at higher elevations (Mitchell & Buffam, 2001; Overhulser et al., 2004).

When the random effect of plot was included in host tree-level models for CDG and SYMP, the models explained a higher amount of variance, suggesting that differences in observed BWA damage and symptoms were influenced by local effects. This is supported by the additional variance explained when landform groups were included. Most likely, this variation among plots and landform groups is due to abiotic factors that differentially affect BWA populations. Likewise, the significant difference among landform groups suggests that there are factors unmeasured in this study that impact BWA infestations and damage at the larger regional scale. These might be differences in climatic variables like temperature or precipitation patterns across a broad spatial scale or be indicative of the overall time that BWA has been active in the area. Although BWA was first detected in northern Utah in 2017 it has likely been in the area for longer.

The first detections within our study area were in southeastern Idaho in 2007, and the first Utah infestation was found in the Wasatch Front in 2017 (Alston et al., 2018; Davis et al., 2020). As such, we could speculate that the Idaho Sky Island landform group (plots that occurred within the disjunct alpine forests of southeastern Idaho) has been infested with BWA longer than the Wasatch Front landform group. BWA was likely in these areas before detection and there was likely some amount of delay from the time of initial infestation to the presentation of symptoms and damage. The Bear River Mountains group was statistically similar to the Idaho Sky Islands group in terms of BWA damage, and significantly different than either the Wasatch Front group or the Uintas group (Figure 2). This may indicate that, while the BWA invasion along the Bear River Mountains occurred at a similar time to the Idaho Sky Islands group and before the other Utah landform groups. If so, then continued assessment of these areas may provide evidence of a “flaming front” pattern with the Bear River Mountains being colonized within a more similar timeframe to fir stands occurring in southeastern Idaho. A better understanding of the coarse, regional dispersal patterns of BWA – such as that it will colonize in a “front” pattern and not “jump” can be used to better direct monitoring efforts in areas where the insect has yet to be detected.

An alternative explanation for the regional differences in BWA damage within the Intermountain region may be compositional or landscape differences at spatial scales larger than measured here. While we did not explicitly set out to assess spatial effects on the spread of BWA, the significance of latitude in the abiotic factor model may be suggestive of a spatial pattern to the severity in our study area. This negative relationship between BWA severity metrics and latitude hints more towards a “flaming front” among the plots we measure where BWA severity increased as plots further south were sampled. Latitude would not inherently be important to the damage caused by an invasive insect and most likely serves as another proxy for these unmeasured relationships — most likely, climatic factors, landscape metrics, or as a rough proxy for the time of infestation. If we were able to consistently determine how long BWA has been present on a tree or in a stand, we may be able to reconstruct how BWA dispersed across the landscape of the study area.

Co-morbidity agents and mortality

There were mixed results regarding the interaction between BWA symptoms and damage and other agents of co-morbidity. No co-occurring pest model performed well in terms of explaining variance between either CDG or SYMP , but some predictor variables were found to be significant. The presence of other pests was frequently found to have low predictive power for BWA-related damage and symptoms. No relationship could be established between the plot-level detection of bark beetle symptoms and estimates of BWA-related damage or even mean tree diameter. This is somewhat unexpected. Both BWA and bark beetles would benefit from co-occurrence with each other via cascading effects on tree defense symptoms. The sampling design likely affects this result. Given concerns about the ability to accurately assess bark beetle activity in live subalpine fir, we used data on bark beetle occurrence from dead trees and at the plot level, and this approach was likely too broad to observe trends given the narrow time frame in which we visited plots. Root and heartwood fungal diseases were associated with increased BWA damage, but this relationship is probably also muddled by sampling techniques. As we did not examine every tree for mycelial fans beneath the root collar, we are most likely significantly underestimated the presence of fungal rots in trees on our plots. If BWA damage continues to be considered in relation to tree size (as we have with our scaled metrics), more research specifically into the relationship between BWA and fungal disease in large trees may elucidate more interactions between the two factors.

The negative relationship between BWA-specific symptoms at the host level and the presence and severity of fir broom rust was a surprising result. Fir broom rust is a fungal parasite that attacks Abies as part of its life cycle. Once the fungus has entered the wood of its host, it induces the production of epicormic sprouts which create what is called the “witch’s broom” growth form. From these epicormic branches, needle production occurs, and spore-producing structures (aecia) are formed on the underside of the needles. These structures produce a foul-smelling odor which has been linked to increased use and landings by certain species of insects (Peterson, 1964), although there have been no reports to suggest this type of relationship for BWA. The negative relationship we found between fir broom rust and BWA severity, however, may be explained by volatile terpenes produced in response to fungal infection. Terpenes are secondary metabolites that conifers use in plant defense (Zulak & Bohlmann, 2010) and can have repellant and fungicidal properties (Kusumoto et al., 2014; Klutsch et al., 2016; Kopaczyk et al., 2020). Indeed, the presence of fir broom rust has been shown to induce the production of secondary volatiles such as certain monoterpenes in Abies (Alexandru et al., 2011). Although the specific mechanism is unclear, our results suggest that trees infected by fir broom rust may have some resistance to BWA infestations. This is especially important as the study area (particularly the Bear River Mountains) is known to be some of the densest areas for fir broom rust in North America (Peterson, 1963). We did not find significance for this relationship at the stand level, however. This may be due, in part, to the high disparity between fir broom rust ratings across all host trees within a plot.

The state of BWA in northern Utah and southeastern Idaho

Across all study plots, gouting was the most dependable way of identifying that a tree had been attacked by BWA. When detected, we used the presence of woollies on the bole to identify active infestations. Roholtz is considered another identification tool and a clear sign of damage to hosts. We did not find evidence of roholtz in our study trees. The reason for this is unclear. The formation of roholtz in the resin ducts of host trees should not inherently be a time-dependent process, but even if numerous generations of BWA are needed to initiate its formation, we are not sure why we did not see it on even a moderate scale.

Unlike the severe mortality events within three years of infestation that Mitchell observed occurring on subalpine fir in the 1950s and 60s in Oregon, we did not observe this pattern in our study plots. Davis et al. (2022) also suggests that there may be a delay in the appearance of tree mortality. Several of our plots have been infested with BWA for at least 3-4 years prior to our study as the infestations were originally discovered by USDA Forest Health Protection in 2017-18. BWA population size has been speculated and shown to be at least somewhat density-dependent (Amman, 1970) similar to hemlock woolly adelgid (McClure, 1991), with a decrease in population size following an initial infestation period and population growth (Figure 5). It is probable that different areas within our study are at different points along this timeline. While it is still possible that large-scale, high-severity tree mortality events may occur, we found no widespread mortality within our study plots.

Our characterization of BWA infestations in northern Utah and southeastern Idaho suggests that its current effect on subalpine fir stands does not resemble the pattern of the high severity, high mortality outbreak observed along the western side of the Cascades in the 50s and 60s (Johnson and Whiteside, 1957; Mitchell, 1966), but it does suggest a clear impact on the subalpine fir forests of the study area which may result in high severity and mortality occurring as the insects time on the landscape increases. A majority of plots were rated less than 0.25 on the examined 0 – 1 damage metrics. It should be noted that values of scaled CDG above 0.50 would be unlikely to occur in nature. At the stand level, mortality among subalpine fir was only detected at 22 plots. When mortality was detected, the mean percentage of total basal area from dead subalpine fir was 18.7% ± 0.04. The climate of our study area can differ greatly from regions where BWA severity has been high particularly in the Pacific Northwest and

Maritime Canada, and it may be more likely to experience extreme temperature events that are believed to be associated with reductions in overwinter survival. However, further examination into the interplay between BWA and climatic factors within the Intermountain region is needed to fully support this explanation. Higher future temperatures due to climate change may decrease the number of days needed for nymphs to develop and reduce the likelihood of extreme low temperature events that kill overwintering nymphs (Quiring et al., 2008).

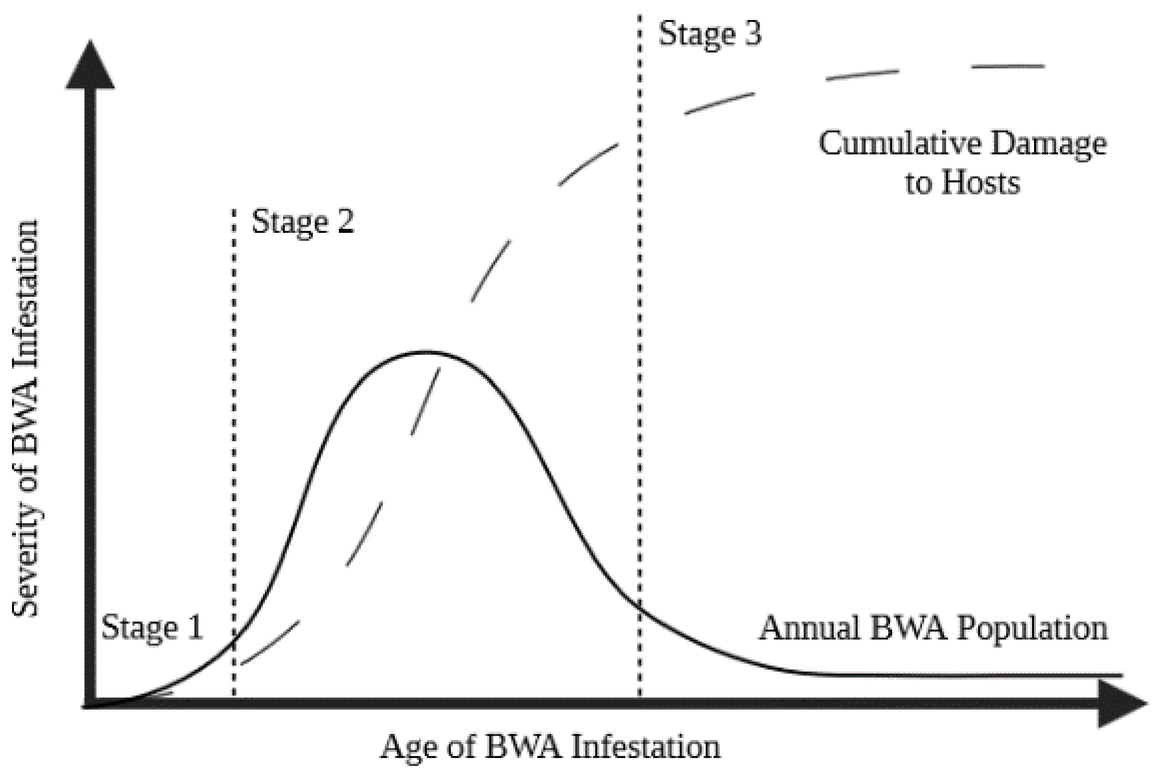

Figure 5: Conceptual model for BWA infestations. Broadly, infestations move through three stages as they age. Stage 1 is characterized by small numbers of BWA and very little or no crown damage. This stage would be unlikely to be detected by monitoring efforts. Stage 2 begins at the onset of noticeable damage to host trees in the stand. It is characterized by the largest number of BWA present and increasing crown damage. While overall population is higher than either Stage 1 or Stage 3, this stage encompasses BWA population growth from few individuals, peak population density, and its decline. Stage 3 is characterized by low numbers of BWA present in the stand and little annual increase in host damage and mortality. BWA can likely remain in this stage for long temporal periods but is not likely to reach peak population again.

Management Implications

The cryptic nature of BWA infestations is likely to prove frustrating for land managers in newly invaded areas of northern Utah. An immediate concern to the correct identification of infestations is the presence of a native adelgid species, *Pineus abietinus* (Underwood & Balch). Subalpine fir is a host to this species and can appear on the boles of trees as woollies much like BWA. However, the insect does not cause the gouting observed in trees infested with BWA. Even when gouting is observed, it would be best to obtain taxonomic or genetic confirmation when possible. No published information exists on the commonality of BWA occurring alongside *Pineus abietinus*, but BWA has been observed occurring alongside another species of native adelgid (personal observation).

The results of this study suggest that gouting may be more common in infested stands within our study area than in other parts of North America. Additionally, the relatively minor level of crown damage that was associated with BWA observed in this study highlights the importance of ground-truthing BWA infestations that have been determined by aerial imagery. In this study, more success in detecting previously unknown BWA infestations was found when looking explicitly for gouting and not, necessarily, large stands of subalpine fir with severe flagging. Examining campsites in areas where subalpine fir was present resulted in several, previously undetected infestations. These infestations occurring at campsites were typically within 15 km of known infestations. It is not clear why this trend was observed. Anthropogenic vectoring of BWA among regional campsites may be an explanation, but more information is needed.

A multifaceted approach where land managers utilize aerial imaging, ground-truthing, coordination with other regional entities monitoring BWA, and positive taxonomic or genetic identification, would be the best practice in the early or continued detection of BWA. Coordination between monitoring efforts from state and federal agencies, local landowners, and the public at large may be necessary to properly understand the regional presence of BWA in a way that any one method of detection cannot achieve. Additionally, a better understanding of the phenological development of BWA within newly invaded areas of northern Utah would be extremely helpful to stakeholders. While the current assumption is that BWA completes at least two generations per year in northern Utah and southeastern Idaho (Alston et al., 2018; Davis et al., 2020), there is likely variation in this among individual trees and infested stands. The two generation per year model suggests that management actions should not occur in spring or fall as these are the times that the lifestage primarily responsible for dispersal (the crawler) is active. Insect development, however, is specifically dictated by temperature. As such, a degree-day model for BWA in the Intermountain region would be of great use.

A stand's structural complexity (modeled by host tree SDI ratio) was the most important predictor of BWA-related damage. Stands where host trees are of an equivalent size to one another saw significantly more BWA-related damage than stands where trees were more likely to differ in size from one another. This is not surprising as resistance to other forest insects has been noted in structurally complex forests (Björkman et al., 2015; Klapwijk et al., 2016). Forest management actions that lower the structural complexity of fir stands, such as thinning from below, may create conditions that increase the risk of substantial BWA-related damage. There exist several broad approaches to stand management (generally falling under the purview of “uneven-aged” management) that may provide some manner of resistance to BWA-related damage but are unlikely to decrease the probability of infestation for individual trees. Once BWA is present in a stand, there is evidence that it can remain present at levels greatly reduced from peak population levels and would be unlikely to be extirpated as long as host species are present (Schooley and Bryant, 1976; Mitchell and Buffam, 2001).

Conclusions

The invasive BWA must now be considered part of the larger subalpine fir mortality complex in northern Utah and southeastern Idaho. Its presence and impact are clear, but at this point in the recent invasion history widespread, high-intensity mortality events have not occurred, at least in our study plots. We found that the presence and maximum severity of fir broom rust was negatively associated with BWA-specific symptoms (gouting and bole infestation), suggesting that high densities of fir broom rust may lessen the spread and severity of BWA. The structure of subalpine fir stands was the most important predictor of BWA-related damage, a finding which can facilitate silvicultural management for reducing vulnerability to BWA. It is our suggestion then that BWA must be considered alongside other agents when analysis of conifer forest susceptibility occurs in this region. Subalpine fir communities are likely full of novel interactions between BWA and other agents of mortality (i.e., bark beetles, fungal pathogens, and windthrow) in ways that have not yet been considered. Regardless, further understanding of BWA and its impact on the forests of the Intermountain region is still in its initial stages, and there needs to be substantially more research in the coming years as it continues to increase its range and (likely) its severity. Understanding the drivers and interactions influencing this insect is critical to addressing future concerns of mortality, especially in conjunction with climate change. Our findings establish some of the host- and stand-level characteristics that are currently influencing BWA-related damage and mortality in the Intermountain region, but many others have yet to be examined. Looking forward, continued research into multiple areas could address gaps in our understanding of BWA:

- Climatic drivers across a variety of spatial scales – especially in comparison to other regions of North America.
- A more detailed understanding of the specific drivers of BWA-related damage and how regional differences may result in unexpected patterns of symptoms, damage, and mortality. A more long-term and specific examination of BWA interactions with other agents of the subalpine fir mortality complex.
- Examination of the spatial patterns of and differences among BWA-infested forests regarding host forest connectivity, edge effects, patchiness, and non-climatic abiotic factors that may contribute to susceptibility at larger spatial extents.
- An understanding of the temporal trends of BWA infestations within recently invaded areas in northern Utah and southeastern Idaho to inform continued eastern spread into true fir forests of Wyoming and Colorado. More specifically, a better understanding of BWA development to aid

managers in the region in deciding what part of the year to apply treatments.

References

Alexander, R. R. 1984. Silvical Characteristics of Subalpine Fir. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Alexander, R. R., and O. Engelby. 1985. Engelmann Spruce - Subalpine Fir. Forest Ecology and Management 11:297.

Alston, Diane. D. McAvoy. 2018, Winter. New Utah Forest Pest: Balsam Woolly Adelgid. Utah Pests Quarterly Newsletter:1–2.

Amman, G. D. 1962. Seasonal Biology of the Balsam Woolly Aphid on Mt. Mitchell, North Carolina. Journal of Economic Entomology 55:96–98.

Amman, G. D. 1966. *Aphidecta obliterata* (Coleoptera: Coccinellidae), an Introduced Predator of the Balsam Woolly Aphid, *Chermes piceae* (Homoptera: Chermidae), Established in North Carolina. Journal of Economic Entomology 59:506–508.

Annand, P. N. 1928. A contribution toward a monograph of the Adelginae (Phylloxeridae) of North America. Stanford University Press, Stanford University, Calif.

Arthur, F. H., and F. P. Hain. 1984. Seasonal history of the balsam woolly adelgid (Homoptera:Adelgidae) in natural stands and plantations of Fraser fir. Journal of Economic Entomology 77:1154–1158.

Arthur, F. H., and F. P. Hain. 1987. Influence of Balsam Woolly Adelgid (Homoptera: Adelgidae) on Monoterpenes Found in Bark and Sapwood of Fraser Fir. Environmental Entomology 16:712–715.

Asaro, C., F. H. Koch, and K. M. Potter. 2023. Denser forests across the USA experience more damage from insects and pathogens. Scientific Reports 13:3666.

Atkins, M. D., and A. A. Hall. 1969. Effect of light and temperature on the activity of balsam woolly aphid crawlers. The Canadian Entomologist 101:481–488.

Balch, R. E. 1932. The “Gout Disease” of Balsam Fir. The Forestry Chronicle 8:46–51.

Balch, R. E. 1952. Studies of the Balsam Woolly Aphid, *Adelges piceae* (Ratz.) and its Effects on Balsam Fir, *Abies balsamea* (L.) Mill. Canada Department of Agriculture, Science Service, Division of Forest Biology.

Balch, R. E., J. Clark, and J. M. Bonga. 1964. Hormonal Action in Production of Tumours and Compression Wood by an Aphid. Nature 202.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Bechtold, W. A., and P. L. Patterson. 2015. The Enhanced Forest Inventory and Analysis Program National Sampling Design and Estimation Procedures. SRS-GTR-80. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Bentz, B. J., A. M. Jönsson, M. Schroeder, A. Weed, R. A. I. Wilcke, and K. Larsson. 2019. *Ips typographus* and *Dendroctonus ponderosae* Models Project Thermal Suitability for Intra- and Inter-Continental Establishment in a Changing Climate. Frontiers in Forests and Global Change 2.

Berg, E. E. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. Forest ecology and management v. 227:219–232.

Björkman, C., H. Bylund, U. Nilsson, G. Nordlander, and M. Schroeder. 2015. Effects of new forest management on insect damage risk in a changing climate. Pages 248–266 *in* C. Björkman and P. Niemelä, editors. Climate change and insect pests. CABI, Wallingford.

Brooks, M. H., J. J. Colbert, R. G. Mitchell, and R. W. Stark. 1987. Western Spruce Budworm. U.S. Department of Agriculture Forest Service.

Burns, R. M., B. H. Honkala, and tech. coords. 1990. Silvics Manual Volume 1-Conifers and Volume 2-Hardwoods. U.S. Department of Agriculture, Forest Service, Washington, DC.

Currano, Ellen. D., P. Wilf, S. L. Long, C. C. Labandeira, E. C. Lovelock, and D. L. Royer. 2008. Sharply increased insect herbivory during the Paleocene–Eocene Thermal Maximum. Proceedings of the National Academy of Sciences of the United States of America 105:1960–1964.

Dancewicz, K., B. Gabryś, I. Morkunas, and S. Samardakiewicz. 2021. Probing behavior of *Adelges laricis* Vallot (Hemiptera: Adelgidae) on *Larix decidua* Mill: Description and analysis of EPG waveforms. PLoS ONE 16:e0251663.

Davis, G. A., L. Lowrey, D. Malesky, T. Eckberg, A. Gannon, and J. Hicke. 2022. Influences of Balsam Woolly Adelgid and Climate on True Fir: A Baseline for Utah and Montana and a 10-year Assessment for Idaho. Page SRS-GTR-266 Potter, Kevin

M.; Conkling, Barbara L., eds. Forest Health Monitoring: national status, trends, and analysis 2021. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Davis, G., L. Lowrey, T. Eckberg, A. Gannon, D. Malesky, and N. Havill. 2020. Notes on balsam woolly adelgid, *Adelges piceae* (Ratzeburg, 1844) (Hemiptera: Adelgidae), range expansion in Idaho, Montana and Utah. The Pan-Pacific Entomologist 96.

Farjon, A. 2011. Abies fraseri. The IUCN Red List of Threatened Species. IUCN Red List of Threatened Species 2013. eT32101A2810241.

Foottit, R. G., and M. Mackauer. 1983. Subspecies of the Balsam Woolly Aphid, *Adelges piceae* (Homoptera: Adelgidae), in North America. Annals of the Entomological Society of America 76:299–304.

Graham, R. T., R. L. Rodriguez, K. M. Paulin, R. L. Player, A. P. Heap, and R. Williams. 1999. The northern goshawk in Utah: Habitat assessment and management recommendations. Page RMRS-GTR-22. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Haeffner, A. D. 1971. Daily Temperatures and Precipitation for Subalpine Forest, Central Colorado. Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Hagle, S. K. 2003. Field Guide to Diseases and Insect Pests of Northern and Central Rocky Mountain Conifers. U.S. Department of Agriculture, Forest Service, State and Private Forestry, Northern Region.

Hain, F. P. 1988. The balsam woolly adelgid in North America. In: Berryman, A.A. (eds) Dynamics of Forest Insect Populations. Population Ecology. Springer, Boston, MA.

Hanley, D. P., W. C. Schmidt, and G. M. Blake. 1975. Stand structure and successional status of two spruce-fir forests in southern Utah. U.S. Department of Agriculture Forest Service:28.

Hansen, E. M. 1996. Western Balsam Bark Beetle, *Dryocoetes confusus* Swaine, Flight Periodicity in Northern Utah. The Great Basin Naturalist 56:348–359.

Harris, J. W. E. 1973. Tree and site characteristics relative to progressive balsam woolly aphid damage to *Abies* spp., British Columbia 1959-1970. Pacific Forestry Research Centre:69.

Harvey, B. J., R. A. Andrus, M. A. Battaglia, J. F. Negrón, A. Orrego, and T. T. Veblen. 2021. Droughty times in mesic places: factors associated with forest mortality vary by scale in a temperate subalpine region. Ecosphere 12.

Havill, N. P., and R. G. Foottit. 2007. Biology and Evolution of Adelgidae. Annual Review of Entomology 52:325–349.

Havill, N. P., B. P. Griffin, J. C. Andersen, R. G. Foottit, M. J. Justesen, A. Caccone, V. D’Amico, and J. S. Elkinton. 2021. Species delimitation and invasion history of the balsam woolly adelgid, *Adelges* (*Dreyfusia*) *piceae* (Hemiptera: Aphidoidea: Adelgidae), species complex. Systematic Entomology 46:186–204.

Hawksworth, F. G., Rocky Mountain Forest and Range Experiment Station (U.S.), and United States. Forest Service. 1977. The 6-class dwarf mistletoe rating system. [Fort Collins, Colo.] : Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Dept. of Agriculture.

Hollingsworth, R. G., and F. P. Hain. 1991. Balsam Woolly Adelgid (Homoptera: Adelgidae) and Spruce-Fir Decline in the Southern Appalachians: Assessing Pest

Relevance in a Damaged Ecosystem. The Florida Entomologist 74:179.

Hrinkevich, K. H., R. A. Progar, and D. C. Shaw. 2016. A Severity Rating System for Evaluating Stand-Level Balsam Woolly Adelgid (Hemiptera: Adelgidae) Damage in Two *Abies* Species in Western North America. Forest Science 62:181–189.

Johnson, N. E., and K. H. Wright. 1957. The balsam woolly aphid problem in Oregon and Washington. Pacific Northwestern Forest and Range Experiment Station.

Keen, F. P. 1952. Insect enemies of western forests. U.S. Department of Agriculture. U.S. Government Printing Office.

Klapwijk, M. J., H. Bylund, M. Schroeder, and C. Björkman. 2016. Forest management and natural biocontrol of insect pests. Forestry 89:253–262.

Klutsch, J. G., A. Najar, P. Sherwood, P. Bonello, and N. Erbilgin. 2017. A Native Parasitic Plant Systemically Induces Resistance in Jack Pine to a Fungal Symbiont of Invasive Mountain Pine Beetle. Journal of Chemical Ecology 43:506–518.

Kopaczyk, J. M., J. Warguła, and T. Jelonek. 2020. The variability of terpenes in conifers under developmental and environmental stimuli. Environmental and Experimental Botany 180:104197.

Kusumoto, N., T. Zhao, G. Swedjemark, T. Ashitani, K. Takahashi, and A.-K. Borg-Karlson. 2014. Antifungal properties of terpenoids in *Picea abies* against *Heterobasidion parviporum*. Forest Pathology 44:353–361.

Lalande, B. M., K. Hughes, W. R. Jacobi, W. T. Tinkham, R. Reich, and J. E. Stewart. 2020. Subalpine fir mortality in Colorado is associated with stand density, warming climates and interactions among fungal diseases and the western balsam bark beetle. Forest Ecology and Management 466:118133.

Lass, L. W., S. P. Cook, B. Shafii, and T. S. Prather. 2014. Development of a Dispersal Model for Balsam Woolly Adelgid, *Adelges piceae* Ratzeburg (Hemiptera: Adelgidae), to Facilitate Landscape-Level Management Planning. International Journal of Forestry Research 2014:1–8.

Little, E. L. 1979. Checklist of United States trees : native and naturalized:iv, 375 p.

Livingston, R. L., J. E. Dewey, D. P. Beckman, and L. E. Stipe. 2000. Distribution of the Balsam Woolly Adelgid in Idaho. Western Journal of Applied Forestry 15:227–231.

Lutz, J. A., T. J. Furniss, D. J. Johnson, S. J. Davies, D. Allen, A. Alonso, K. J. Anderson-Teixeira, A. Andrade, J. Baltzer, K. M. L. Becker, E. M. Blomdahl, N. A. Bourg, S. Bunyavejchewin, D. F. R. P. Burslem, C. A. Cansler, K. Cao, M. Cao, D. Cárdenas, L. Chang, K. Chao, W. Chao, J. Chiang, C. Chu, G. B. Chuyong, K. Clay, R. Condit, S. Cordell, H. S. Dattaraja, A. Duque, C. E. N. Ewango, G. A. Fischer, C. Fletcher, J. A. Freund, C. Giardina, S. J. Germain, G. S. Gilbert, Z. Hao, T. Hart, B. C. H. Hau, F. He, A. Hector, R. W. Howe, C. Hsieh, Y. Hu, S. P. Hubbell, F. M. Inman-Narahari, A. Itoh, D. Janík, A. R. Kassim, D. Kenfack, L. Korte, K. Král, A. J. Larson, Y. Li, Y. Lin, S. Liu, S. Lum, K. Ma, J. Makana, Y. Malhi, S. M. McMahon, W. J. McShea, H. R. Memiaghe, X. Mi, M. Morecroft, P. M. Musili, J. A. Myers, V. Novotny, A. de Oliveira, P. Ong, D. A. Orwig, R. Ostertag, G. G. Parker, R. Patankar, R. P. Phillips, G. Reynolds, L. Sack, G. M. Song, S. Su, R. Sukumar, I. Sun, H. S. Suresh, M. E. Swanson, S. Tan, D. W. Thomas, J. Thompson, M. Uriarte, R. Valencia, A. Vicentini, T. Vrška, X. Wang, G. D. Weiblen, A. Wolf, S. Wu, H. Xu, T. Yamakura, S. Yap, J. K. Zimmerman, and A. Kerkhoff. 2018. Global importance of large-diameter trees. Global Ecology and Biogeography

27:849–864.

van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. Science 323:521–524.

Marini, L., M. P. Ayres, and H. Jactel. 2022. Impact of Stand and Landscape Management on Forest Pest Damage. Annual Review of Entomology 67:181–199.

McClure, M. S. 1991. Density-Dependent Feedback and Population Cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. Environmental Entomology 20:258–264.

McDonald, G. I. 1987. Armillaria in the Northern Rockies: Pathogenicity and Host Susceptibility on Pristine and Disturbed Sites. U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Mitchell, R. G., N. E. Johnson, and J. A. Rudinsky. 1961. Seasonal History of the Balsam Woolly Aphid in the Pacific Northwest. The Canadian Entomologist 93:794–798.

Moreno, A., E. Garzo, G. Fernandez-Mata, M. Kassem, M. A. Aranda, and A. Fereres. 2011. Aphids secrete watery saliva into plant tissues from the onset of stylet penetration. Entomologia Experimentalis et Applicata 139:145–153.

Morin, R. S., A. M. Liebhold, and K. W. Gottschalk. 2009. Anisotropic spread of hemlock woolly adelgid in the eastern United States. Biological Invasions 11:2341–2350.

North, M. P., R. E. Tompkins, A. A. Bernal, B. M. Collins, S. L. Stephens, and R. A. York. 2022. Operational resilience in western US frequent-fire forests. Forest

Ecology and Management 507:120004.

Overhulser, David. L., I. R. Ragenovich, M. McWilliams, and E. A. Willhite. 2004. Balsam Woolly Adelgid Occurrence on True Fir in Oregon. Pest Management Report, Oregon Department of Forestry.

Peterson, R. S. 1963. Effects of Broom Rusts on Spruce and Fir. Intermountain Forest & Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Peterson, R. S. 1964. Fir Broom Rust. U.S. Department of Agriculture, Forest Service.

Puritch, G. S. 1971. Water Permeability of the Wood of Grand Fir (*Abies grandis* (Doug.) Lindl.) in Relation to Infestation by the Balsam Woolly Aphid, *Adelges piceae* (Ratz.). Journal of Experimental Botany 22:936–945.

Quiring, D., D. Ostaff, L. Hartling, D. Lavigne, K. Moore, and I. DeMerchant. 2008. Temperature and plant hardiness zone influence distribution of balsam woolly adelgid damage in Atlantic Canada. The Forestry Chronicle 84:558–562.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ragenovich, I. R., and R. G. Mitchell. 2006, May. Balsam Woolly Adelgid. U.S. Department of Agriculture Forest Service.

Rideout, E. L., D. Alston, B. J. Bentz, and C. von Dohlen. Phenology of the Invasive Balsam Woolly Adelgid, Adelges piceae, on Subalpine Fir in Northern Utah (Unpublished manuscript). Utah State University, Department of Biology.

Schomaker, M. E., S. J. Zarnoch, W. A. Bechtold, D. J. Latelle, W. G. Burkman, and S. M. Cox. 2007. Crown-condition classification: a guide to data collection and analysis. Page SRS-GTR-102. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Schooley, H. O., and D. G. Bryant. 1976. The Balsam Woolly Aphid in Newfoundland. Newfoundland Forest Research Centre.

Sharov, A. A., B. C. Pijanowski, A. M. Liebhold, and S. H. Gage. 1999. What affects the rate of gypsy moth (Lepidoptera: Lymantriidae) spread: winter temperature or forest susceptibility? Agricultural and Forest Entomology 1:37–45.

Skovsgaard, J. P., and J. K. Vanclay. 2008. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. Forestry 81:13–31.

Skulason, B., O. K. Hansen, I. M. Thomsen, V. Talgø, and U. B. Nielsen. 2017. Damage by *Neonectria neomacrospora* and *Adelges piceae* in provenance trials of subalpine fir (*Abies lasiocarpa*) in Denmark. Forest Pathology 47:e12326.

Sonmez, T., S. Keles, and F. Tilki. 2007. Effect of aspect, tree age and tree diameter on bark thickness of *Picea orientalis*. Scandinavian Journal of Forest Research 22:193–197.

Stängle, S. M., and C. F. Dormann. 2018. Modelling the variation of bark thickness within and between European silver fir (*Abies alba* Mill.) trees in southwest Germany. Forestry: An International Journal of Forest Research 91:283–294.

Stock, A. J. 1991. Western Balsam bark beetle, *Dryocoetes confusus* Swaine : impact and semiochemical-based management. Simon Fraser University.

Thornthwaite, C. W. 1948. An Approach toward a Rational Classification of Climate:49.

Toney, C., and M. C. Reeves. 2009. Equations to Convert Compacted Crown Ratio to Uncompacted Crown Ratio for Trees in the Interior West. Western Journal of Applied Forestry 24:76–82.

Varty, I. W. 1956. Adelges Insects of Silver Firs. Forestry Commission Bulletin 26.

Werstak, C. E., J. D. Shaw, S. A. Goeking, C. Witt, J. Menlove, M. T. Thompson, R. J. DeRose, M. C. Amacher, S. Jovan, T. A. Morgan, C. B. Sorenson, S. W. Hayes, and C. P. McIver. (2016). Utah's forest resources, 2003-2012. Resour. Bull. RMRS-RB-20. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 159 p.

Westing, A. H. 1968. Formation and Function of Compression Wood in Gymnosperms. II. Botanical Review 34:51–78.

Williams, A. P., C. D. Allen, A. K. Macalady, D. Griffin, C. A. Woodhouse, D. M. Meko, T. W. Swetnam, S. A. Rauscher, R. Seager, H. D. Grissino-Mayer, J. S. Dean, E. R. Cook, C. Gangodagamage, M. Cai, and N. G. McDowell. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292–297.

Windmuller-Campione, M. A., J. DeRose, and J. N. Long. 2021. Landscape-Scale Drivers of Resistance and Resilience to Bark Beetles: A Conceptual Susceptibility Model. Forests 12:798.

Zhang, J., K. A. Finley, N. G. Johnson, and M. W. Ritchie. 2019. Lowering Stand Density Enhances Resiliency of Ponderosa Pine Forests to Disturbances and Climate Change. Forest Science 65:496–507.

Zilahi-Balogh, G. M. G., L. M. Humble, R. Foottit, and A. Stock. 2016. History of the balsam woolly adelgid, Adelges piceae (Ratzeburg), in British Columbia, with notes on a recent range expansion. Journal of the Entomological Society of British Columbia 113.

Zulak, K. G., and J. Bohlmann. 2010. Terpenoid Biosynthesis and Specialized Vascular Cells of Conifer Defense. Journal of Integrative Plant Biology 52:86–97.

CHAPTER 3

A MODEL FOR ASSESSING STAND HAZARD FOR BALSAM WOOLLY ADELGID IN NORTHERN UTAH AND SOUTHEASTERN IDAHO

Abstract

The invasive forest insect, *Adelges piceae* (Ratz.), commonly known as the balsam woolly adelgid (BWA), poses a significant threat to subalpine fir populations in recently invaded areas of northern Utah and southeastern Idaho . However, the lack of a region-specific hazard rating system for predicting BWA-related damage serves as a hindrance to establishing effective management strategies. In this study, we aimed to develop a hazard rating model that incorporates stand conditions and climate factors to predict BWA-related damage at the stand-level. We collected data on stand structure, composition, and BWA-related damage indicators from multiple plots in Utah, Idaho, and Wyoming. Using regression analysis, we identified key stand level characteristics, including host tree structural metrics, that were strong predictors of BWA severity. We also incorporated climatic factors, such as autumn precipitation, into our model to refine predictions. This model served as the principal component of a three-tiered hazard rating system that categorizes subalpine fir stand into three levels of risk of BWA-related damage into light, moderate, and heavy levels, providing land managers with valuable information for preemptive management strategies. We provide additional guidance and suggestions on BWA monitoring and management as populations continue to spread east and south into Utah. Our findings highlight the importance of considering stand

conditions and abiotic factors when assessing the potential impact of BWA on subalpine forests.

Introduction

Adelges piceae (Ratz.) is an invasive forest insect native to central and southern Europe that was first detected in Utah in 2017 (Alston et al. 2018). Balsam woolly adelgid (BWA) is an obligate, herbivore of true firs (*Abies* spp.) in both its native and introduced range. While it is not a significant pest in its native range in Europe, it has been identified as the cause of extensive damage in true fir populations in North America and North American species planted in Europe (Balch 1952, Varty 1956, Skulason et al. 2016). Subalpine fir, *Abies lasiocarpa* [Hook] Nutt., has been identified as the host species most at risk to experience high-intensity damage and mortality in western North America (Hain 1988). With continued range expansion into Utah and Wyoming expected, we were interested in developing a hazard rating model for predicting BWA-related damage at the stand level when BWA is present.

For much of the history of silvicultural management in North America, many managers and scientists have noted the conditions in which severe insect outbreaks occur. Hazard rating systems rely on the structure, density, and composition of stands to estimate the level of insect-related damage expected and have been important tools in the management of damaging forest insects (Shore and Safranyk 1992, Bentz et al. 1993, Koch et al. 2006, Baier et al. 2007). BWA, however, lacks an established, published history of the impacts of stand conditions on BWA-related damage. BWA populations do not appear to be eruptive or ‘outbreak’ in the way that some bark beetle populations do

(Chapter 2). Some authors have noted that BWA symptoms appear to be affected by the elevation of the forest where infestations occur (Schooney and Bryant 1976, Overhulser et al. 2004). Likewise, better site conditions (high soil productivity, optimal climate conditions) have been linked to more severe damage (Mitchell & Buffam 2001, Overhulser et al. 2004). However, much of what we know about BWA's interactions with non-climatic factors is from areas in the U.S. Pacific Northwest and Maritime Canada (Harris 1973, Page 1975). As such, there is a need for a region-specific hazard rating system for predicting BWA-related damage in newly invaded areas of northern Utah and southeastern Idaho.

In Chapter 2, we provided evidence that – on the whole – invasive BWA-related damage and mortality in our study plots do not appear to be at the level of an outbreak on the scale and severity of what was historically found in the US Pacific Northwest (Johnson and Wright 1957, Mitchell 1966). In the coming decades, however, BWA is likely to cause significant amounts of damage to subalpine forests as it expands throughout Utah and surrounding states. It is important for stakeholders to act preemptively when possible to minimize the potential for high-severity infestations of BWA, and they can do so, in part, by taking steps to increase the structural complexity of host trees within their stands. To provide forest managers with a tool to aid in this effort, we seek to develop a hazard rating system for BWA utilizing stand conditions and abiotic factors.

Methods

Study sites and data collection

The study plots and data collection methodology used the same approach as Chapter 2. Plots were located primarily throughout Utah and southeastern Idaho (Figure 6). Study plots were designed as an 11.35 m radius circle (representing 1/250th of a hectare) and overstory trees (≥ 12.7 cm in diameter at breast height, 1.37 m, DBH) that fell within the plot were sampled. Estimates were collected for metrics describing tree size and crown injury (Chapter 2)

Analytical assessment

To estimate BWA-related damage, we developed a simplified index describing crown damage and including gouting to help separate the impact of BWA from other potential causes of crown damage.

To do this, we averaged crown dieback and flagging across vertical thirds of the tree height and divided by five (the maximum rating possible) to create a 0-1 index describing each factor. Gouting ratings were averaged to create a 0-1 index as well. These three variables were then averaged to create a single 0-1 index describing crown damage and gouting (CDG).

$$CDG = \frac{\left(\frac{Dieback}{5}\right) + \left(\frac{Flagging}{5}\right) + \left(\frac{Gouting}{3}\right)}{3}$$

Because a majority of a stand's aboveground biomass is comprised of the largest trees in the stand, we scaled CDG by individual-tree basal area to reflect their relative importance at plots (Lutz et al. 2018).

For tree$_j$ on plot$_i$: $CDG \times \frac{Basal\ Area_{ji}}{\max(Basal\ Area_i)}$

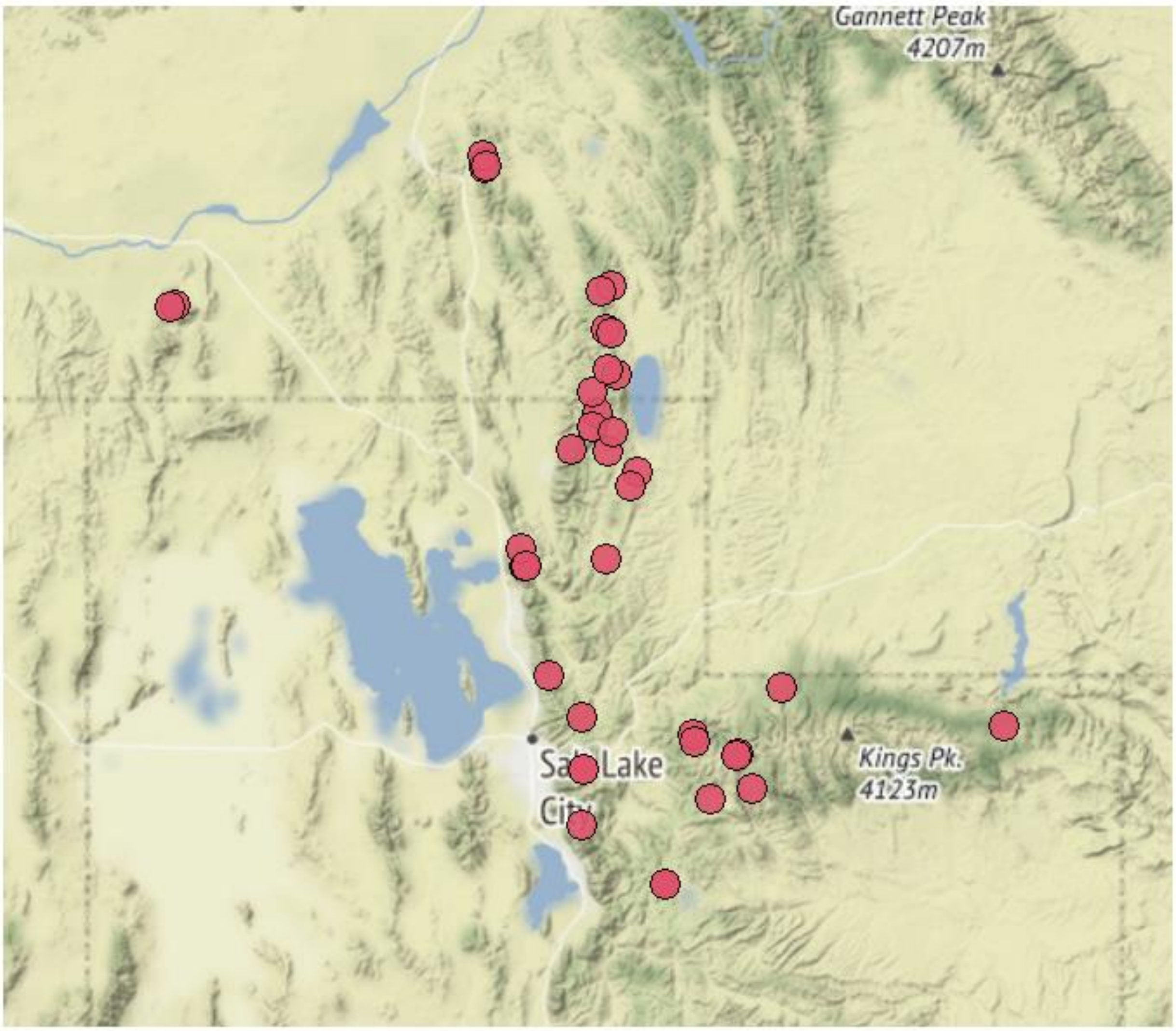

Figure 6: Map displaying study sites within Utah and southeastern Idaho (n = 39).

At the stand-level, several metrics that characterized stand structure and composition were calculated (Table 11). Relevant to the hazard rating model, we calculated Reineke's stand density index (SDI_R), additive stand density index (SDI_Σ), and relative SDI. SDI_R is calculated as a mean and considers the average size of trees and number of them that occur on a plot, and SDI_Σ is the summation of the SDI_R when calculated for each individual tree on a plot. To characterize stand structure, we also calculated quadratic mean diameter (QMD) and the SDI ratio (a plot's SDI_R divided by its SDI_Σ) for host trees.

Table 11: Summary statistics, i.e., mean, standard error of the mean (SE), and the range of values, of forest structure metrics used in assessing relationships between BWA infestation and stand characteristics. Additional non-climatic abiotic factors are summarized below.

Metric		Mean ± SE	Range
Reineke's Stand Density Index			
	Host	170 ± 15.7	25 — 496
	Total	220 ± 17.9	25 — 588
Summed Stand Density Index			
	Host	159 ± 14.9	24 — 469
	Total	210 ± 17.0	24 — 555
Stand Density Index Ratio			
	Host	0.96 ± 0.003	0.93 — 0.99
	Total	0.96 ± 0.003	0.89 — 0.99
Quadratic Mean Diameter (cm)			
	Host	29.0 ± 1.1	16.0 — 45.8
	Total	30.7 ± 1.2	18.6 — 53.8
	Host-Total Ratio	0.95 ± 0.01	0.64 —1.08
Basal Area (m^3/ha)			
	Host	22.5 ± 2.4	3.0 — 73.5
	Total	30.3 ± 2.8	3.0 — 89.1
	Host-Total Percentage	76.2 % ± 0.04	17.3 — 100 %
Trees per Hectare			
	Host	324 ± 23.0	74 — 717
	Total	404 ± 28.6	74 — 890
	Host-Total Percentage	82.7 % ± 0.03	33.3 — 100 %
Topographic			
	Elevation (m)	2374 m ± 55.8	1816 – 3210 m
	Slope	22.72 % ± 1.85	2 — 54 %
	Folded aspect	60.4° ± 8.36	1 — 177°

In Chapter 2, we used linear multiple regression to identify relationships between stand-level characteristics and BWA-related damage. As our response variable, we selected CDG. We applied a natural log transformation to CDG to meet assumptions of normality and homoscedasticity and tested groups of predictor variables based on their shared qualities, i.e., abiotic factors or host-specific metrics. The strongest predictor variables were then included within a best-performing model. This composite model included host SDI ratio and host QMD (describing structure) and relative SDI (describing stocking/density). Latitude was also selected as part of the composite model but is not included here due to concerns over the future applications of latitude as it likely serves as a proxy for unmeasured temporal or climatic factors.

To further refine our model and account for the impact that abiotic factors have on the severity of BWA, we have also included a climatic term in our composite model. 30-year normals (from 1991-2020) of climatic variables were gathered from ClimateNA (version 7.31) at a resolution of 800 x 800 m. A Pearson rank-order correlation matrix was then calculated to determine the most impactful and significant climate predictors that were independent of each other. We identified three potential terms: autumn precipitation (PPT-A), summer precipitation (PPT-S), and maximum temperature in winter (TMAX-W). These three terms were then included in our composite model, and AIC was used to choose one term out of the three. We chose to only incorporate one term to maintain parsimony within the model.

Using CDG as our damage metric, we identified three levels of BWA-related damage at our plots – light, moderate, and heavy. These levels were identified in R 4.2.1 (R Core Team 2022) by using the package “optbin” (v. 1.2, Krieder 2022) which binned data into three levels to minimize the mean squared error. Three levels were used to prevent any hazard level from having too few plots within it. These hazard levels were then evaluated with one-way ANOVA to indicate significance in the means of independent variables between groups. If the ANOVA indicated significance, then Tukey HSD tests were run as well.

Results

Study plots had a mean scaled CDG rating of 0.13 ± 0.01 with a range from 0.04 to 0.25. For any of the three climatic variables, the tested model remained significant ($P < 0.01$) with their inclusion. PPT-S was the only climate term that was not significant in its respective model. PPT.A had the highest coefficient (in absolute value) across the three climatic terms (Table 12).

Table 12: Linear multiple regression model for predicting BWA-related damage in subalpine fir stands. The model includes predictor variables related to stand structure, stand density, and climate. The response variable is the crown damage and gouting (CDG) index with the basal area scalar. The model's performance is evaluated using the adjusted R-squared value and Akaike Information Criterion (AIC).

Model: PPT-A		Est. Coef.	SE	*T*
	Intercept	-18.86	1.78	-10.6
	Host SDI ratio	15.84	1.81	8.77
	Host QMD	0.07	0.02	4.33
	Relative SDI	-0.98	0.21	-4.57
	PPT-A (cm)	0.05	0.01	3.86
$F(4,34)$ = 32.88	AIC: -9.0	$P < 0.01$	Adj. $R^2 = 0.77$	

The model including PPT.A also had the lowest AIC at -9.0 (PPT.S = 3.0, TMAX.W = -0.8) and resulted in an adj. R^2 of 0.77. This best-performing model is:

$$CDG = e^{-18.9 + 15.8(host\ SDI\ ratio) + 0.07(host\ QMD) + 0.05(PPT.A) - 0.98(relative\ SDI)}$$

Plots were then divided into three levels by their scaled CDG value denoted as light, moderate, and heavy (Table 13, Figure 7). One-way ANOVAs showed all input terms except for autumn precipitation had significant differences in means between the BWA hazard levels. The Tukey HSD tests conducted for host SDI ratio, relative SDI, and host QMD showed that there were significant differences between the means of the light level and the moderate and heavy levels. Significant differences between the "moderate" and "heavy" levels were only detected for the host QMD input term (Figure 8).

Table 13: Hazard levels assigned using the linear multiple regression model for predicting BWA-related damage in subalpine fir stands. The hazard levels are categorized into three distinct classes: low, moderate, and high. Each level corresponds to the predicted risk of BWA-related damage in the subalpine fir stands. The classification is based on the minimization of the mean standard error.

BWA hazard rating level	*n*	Mean CDG ± SE	CDG range
Light	14	0.081 ± 0.005	≤ 0.106
Moderate	17	0.137 ± 0.004	0.107 – 0.179
Heavy	8	0.213 ± 0.009	≥ 0.180

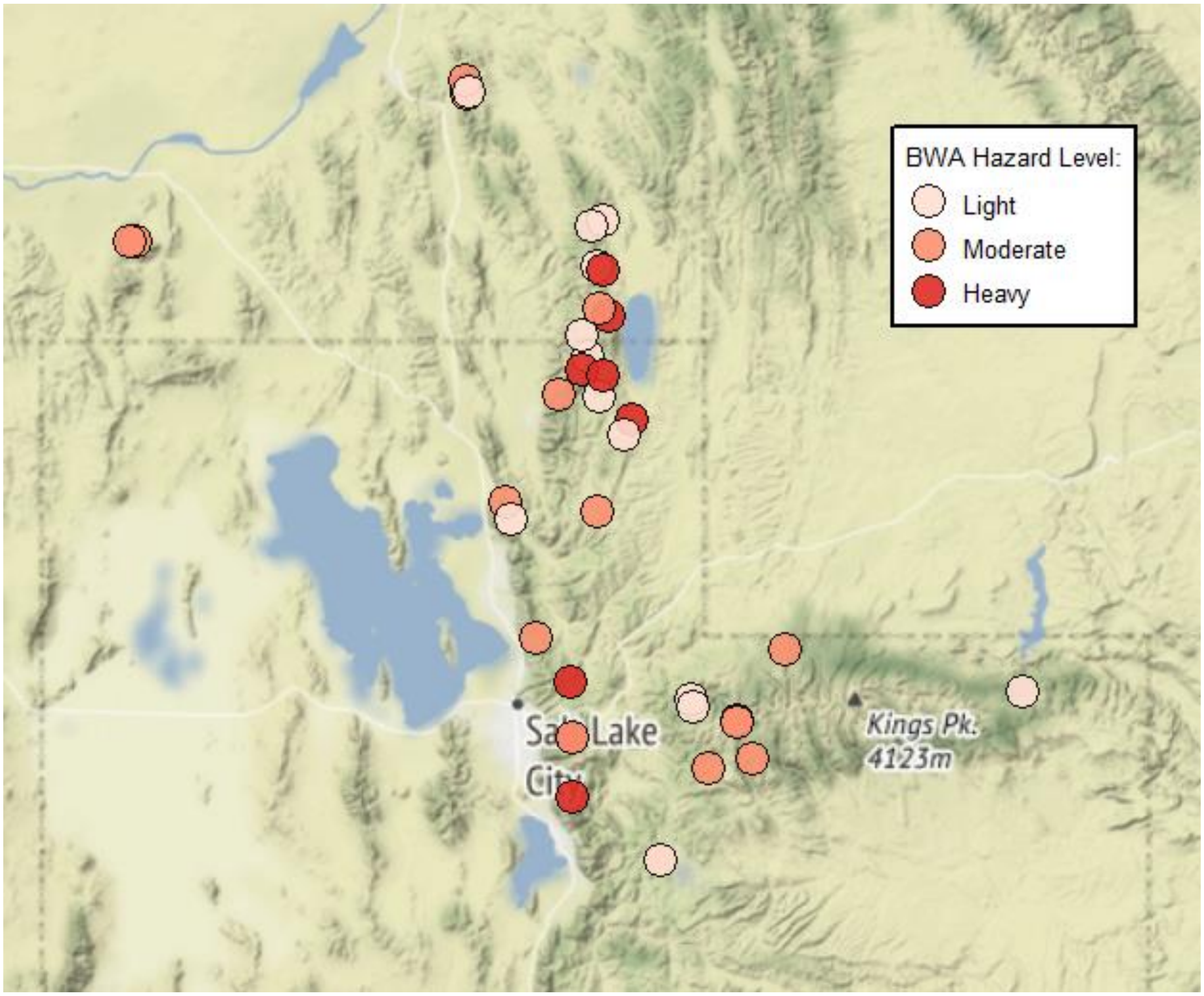

Figure 7: Map illustrating the study sites with assigned BWA hazard level, categorized based on their observed damage using scaled CDG.

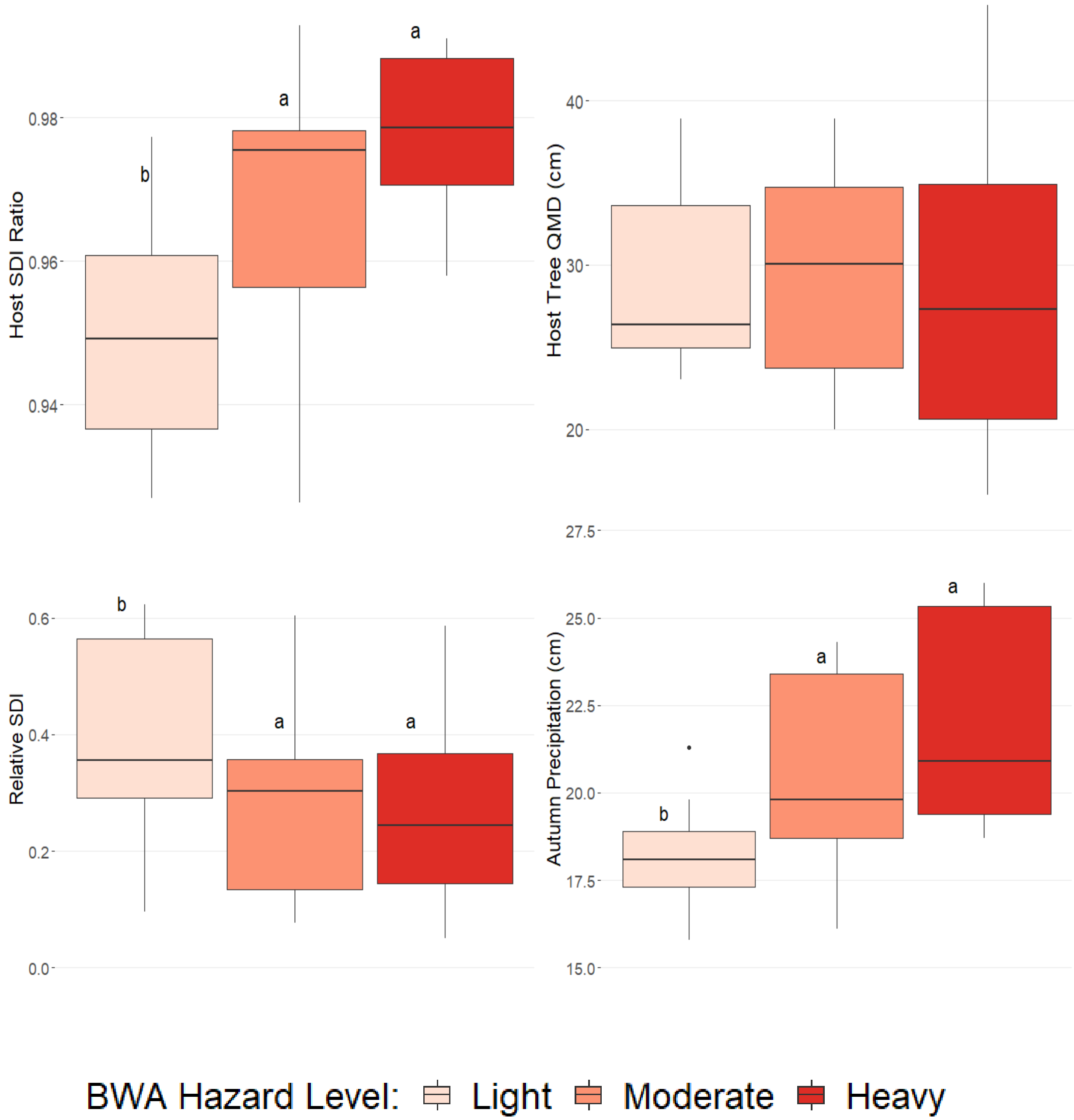

Figure 8: Box and whisker plots showing the mean values of input terms across the three BWA hazard levels. Significant differences are indicated by different letters above boxplots.

Discussion

We sought to develop a rating system for BWA that relates the observed severity of BWA-related damage to stand conditions of subalpine fir in study plots located in northern Utah and southeastern Idaho. Based on our previous work (Chapter 2), damage estimates indicated that BWA-related damage in our study area rarely exceeds one-fourth of the maximum damage value (though stand ratings above 0.50 would be very infrequent in vivo). Likewise, mortality occurred at a majority of plots (22 of 39) but was infrequently more than 25% of a stand's total basal area. However, the long-term ramifications of BWA's presence on the landscape and interactions with other agents of co-morbidity have yet to be observed.

Rating systems for BWA have often focused on the assessment and categorization of a stand's infestation severity via tree damage and mortality (Harris 1973, Schooley and Bryant 1978, Hrinkevich et al. 2016). While such systems are important in understanding the ecological impact of the insect, they do not provide land managers with information regarding expected damage. Previous studies in other regions (Pacific Northwest and Maritime Canada) have attempted to document relationships between stand conditions and BWA impact, but these results appear to be region-specific and lose relevance when applied to other areas (i.e., the significant climatic and topographic differences between northern Utah and Nova Scotia) (Harris 1973, Schooley and Bryant 1978). While not reported in our results, we found it important to note that these relationships are present between stand characteristic terms (e.g., host SDI ratio and relative SDI) and our unscaled damage metric – though with less power. Our rating system's inclusion of common descriptors of stand conditions enables land managers to make more informed decisions in the management of BWA in the Intermountain region.

The host tree SDI ratio at the plot level (the 0-1 ratio created by dividing the additive SDI by Reineke's SDI for only host trees) was the strongest predictor of BWA severity. As such, it is the primary variable responsible for the prediction of hazard. Additional terms in the model include host QMD and relative SDI. Relative SDI is a metric describing the stocking of stands which is calculated by dividing the additive SDI by the maximum SDI for that specific species. The low power, positive relationship between BWA-related damage and host QMD suggests that stands with larger average hosts may be more susceptible to BWA, but this trend is not present when considering individual trees.

There are several potential explanations for why BWA-related damage is positively correlated with autumn precipitation. Autumn precipitation may fall as snow which, when accumulated on the branches of the crown, may serve to insulate BWA during the settling and early development of nymphs. Earlier and heavier snows may also lower the severity of extreme low temperature events that can kill overwintering nymphs. For the relative SDI, host SDI ratio, and autumn precipitation variables in the hazard rating model, one-way ANOVA analysis showed that there were significant differences in the means of stands rated "light" and "moderate." Likewise, these variables could not be shown to have significant differences between the "moderate" and "heavy" ratings. We suggest that this is not necessarily due to the lack of a distinct relationship between the two, but instead that it is a product of a lack of high severity stands in the study area (stands similar in infestation intensity to those in the Pacific Northwest and the southern Appalachians as shown in Johnson and Wright 1957, Mitchell 1966, and Hain 1988).

In Chapter 2, we suggested a link between the presence of fir broom rust and lower severity of BWA-specific symptoms at the individual level. This relationship loses predictive power at the stand level, but the novel interactions between these two agents of subalpine fir mortality should be considered when making management decisions. Trees with mild infestations of fir broom rust (using our adapted dwarf mistletoe rating system from Hawksworth et al. 1977) could have more success repelling BWA attack than trees that are uninfested with broom rust, but this is still speculative. When making land management decisions for subalpine fir-dominated stands, a best practice may be to diversify stand structure to protect against western balsam bark beetle, Armillaria root rot and other fungal pathogens, defoliators such as spruce budworm, and unfavorable climate conditions. Stands with high structural complexity have been shown to provide resistance and resilience to multiple mortality agents (Björkman et al. 2015, Klapwijk et al. 2016).

BWA infestations exhibit a high degree of variability, making it difficult to predict their severity in any given stand with certainty. Forest managers should view the hazard rating as a potential outcome based on the stand's characteristics rather than a guaranteed outcome. Additionally, the duration of the infestation is likely to impact the observed damage. The mean length of infestation at our plots may have been short enough to affect our ability to accurately predict the hazard. Although we have no reason to suspect our sampled stands do not represent a range of different infestation ages, we cannot confirm this. In Oregon, subalpine fir stands infested with BWA saw 40 - 79% mortality over 35 - 45 years (Overhulser et al. 2004). More recent studies including Oregon, Washington, and Idaho have noted a wide range of mortality rates over shorter periods (Hrinkevich et al. 2016, Davis et al. 2022, Hicke et al. 2023). We know that

BWA was detected in Utah in 2017 and was likely present some years before that (Alston et al. 2018, Davis et al. 2020, Chapter 2).

In a managerial context, the results of our characterization of BWA-related damage and the model performance and results suggest that simply thinning from below is not likely to be effective in decreasing a stand’s hazard. The most important predictor of damage was structural complexity. If a land manager thins from below, they may be lowering the structural complexity of a stand and, in turn, increasing the stand’s hazard. Land managers may benefit from a two-fold approach where 1.) trees exhibiting signs of BWA infestation are culled in the winter or, less preferably, the height of summer to avoid seasons (mid-late spring and fall) where increased numbers of crawlers (the life stage primarily responsible for dispersal) are present in infested stands, and 2.) management applications are specifically targeted toward increasing the structural complexity of stands.

While we are unable to provide exact recommendations for treatment options, the negative relationship between BWA-related damage and host SDI ratio agrees with research into other forest insect pests, and diversifying stand structure should be considered as a preventative action that may be done before the insect is present. However, in stands where BWA is already present (as may be determined by the presence of gouting and bole infestations), intermediate treatments are not likely to be effective as previous studies have noted the long-term persistence of BWA in stands (Mitchell & Buffam 2001, Overhulser et al. 2004). In pure fir stands, the most effective measure may be annual or bi-annual monitoring efforts to assess the severity of the infestation (through the assessment of gouting or crown damage) to ensure BWA populations do not exceed light infestation levels. When the stands exceed light levels of infestation, a significant thinning of the most severely infested trees (by gouting, visible bole/crown infestation, or crown damage) may lessen the hazard of the remaining (apparently) uninfested. This is unlikely to fully extirpate the insect from the stand. Total regeneration of the stand remains an option as well in heavily infested/damaged stands and may lower the risk associated with excessive amounts of standing dead in western conifer forests.

Conclusion

This study addressed the need for a region-specific hazard rating system to predict BWA-related damage in subalpine fir stands. Through a combination of stand-level characteristics and climate factors, we developed a predictive model that can assist land managers in making informed decisions to preemptively mitigate the impact of BWA infestations. Our results emphasize the significance of host tree structural metrics in determining the severity of BWA-related damage. Additionally, we highlighted the potential interactions between BWA and other agents of co-morbidity, such as fir broom rust, and emphasized the importance of a multi-faceted approach in directing monitoring efforts. It is important to note that the hazard rating system should be considered as a potential outcome based on stand characteristics rather than a guaranteed outcome, and the duration of infestation may influence the observed damage. Overall, this study provides a valuable tool for forest managers to proactively manage BWA infestations and protect subalpine fir populations in the Intermountain region.

References

Alston, D. and D. McAvoy. 2018, Winter. New Utah Forest Pest: Balsam Woolly Adelgid. Utah Pests Quarterly Newsletter:1–2.

Baier, P., J. Pennerstorfer, and A. Schopf. 2007. PHENIPS—A comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. Forest Ecology and Management 249:171–186.

Balch, R. E. 1952. Studies of the Balsam Woolly Aphid, *Adelges Piceae* (Ratz.) and its Effects on Balsam Fir, *Abies Balsamea* (L.) Mill. Canada Department of Agriculture, Science Service, Division of Forest Biology.

Bentz, B. J., G. D. Amman, and J. A. Logan. 1993. A critical assessment of risk classification systems for the mountain pine beetle. Forest Ecology and Management 61:349–366.

Björkman, C., H. Bylund, U. Nilsson, G. Nordlander, and M. Schroeder. 2015. Effects of new forest management on insect damage risk in a changing climate. Pages 248–266 *in* C. Björkman and P. Niemelä, editors. Climate change and insect pests. CABI, Wallingford.

Davis, G. A., L. Lowrey, D. Malesky, T. Eckberg, A. Gannon, and J. Hicke. 2022. Influences of Balsam Woolly Adelgid and Climate on True Fir: A Baseline for Utah and Montana and a 10-year Assessment for Idaho. Page SRS-GTR-266 Potter, Kevin M.; Conkling, Barbara L., eds. Forest Health Monitoring: national status, trends, and analysis 2021. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Davis, G., L. Lowrey, T. Eckberg, A. Gannon, D. Malesky, and N. Havill. 2020. Notes on balsam woolly adelgid, *Adelges piceae* (Ratzeburg, 1844) (Hemiptera: Adelgidae), range expansion in Idaho, Montana and Utah. The Pan-Pacific Entomologist 96.

Hain, F. P. 1988. The balsam woolly adelgid in North America. In: Berryman, A.A. (eds) Dynamics of Forest Insect Populations. Population Ecology. Springer, Boston, MA.

Harris, J. W. E. 1973. Tree and site characteristics relative to progressive balsam woolly aphid damage to *Abies* spp., British Columbia 1959-1970. Pacific Forestry Research Centre:69.

Hawksworth, F. G., Rocky Mountain Forest and Range Experiment Station (U.S.), and United States. Forest Service. 1977. The 6-class dwarf mistletoe rating system. [Fort Collins, Colo.] : Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Dept. of Agriculture.

Hicke, J. A., G. Davis, L. Lowrey, B. Xu, E. Smirnova, and L. Kalachev. 2023. An evaluation of climate influences on balsam woolly adelgid infestations in Idaho. Forest Ecology and Management 534:120849.

Hrinkevich, K. H., R. A. Progar, and D. C. Shaw. 2016. A Severity Rating System for Evaluating Stand-Level Balsam Woolly Adelgid (Hemiptera: Adelgidae) Damage in Two *Abies* Species in Western North America. Forest Science 62:181–189.

Johnson, N. E., and K. H. Wright. 1957. The balsam woolly aphid problem in Oregon and Washington. Pacific Northwestern Forest and Range Experiment Station.

Klapwijk, M. J., H. Bylund, M. Schroeder, and C. Björkman. 2016. Forest management and natural biocontrol of insect pests. Forestry 89:253–262.

Koch, F. H., H. M. Cheshire, and H. A. Devine. 2006. Landscape-Scale Prediction of Hemlock Woolly Adelgid, *Adelges tsugae* (Homoptera: Adelgidae), Infestation in the Southern Appalachian Mountains. Environmental Entomology 35.

Kreider, G. 2022, September 19. optbin: Optimal Binning of Data.

Lutz, J. A., T. J. Furniss, D. J. Johnson, S. J. Davies, D. Allen, A. Alonso, K. J. Anderson-Teixeira, A. Andrade, J. Baltzer, K. M. L. Becker, E. M. Blomdahl, N. A. Bourg, S. Bunyavejchewin, D. F. R. P. Burslem, C. A. Cansler, K. Cao, M. Cao, D. Cárdenas, L. Chang, K. Chao, W. Chao, J. Chiang, C. Chu, G. B. Chuyong, K. Clay, R. Condit, S. Cordell, H. S. Dattaraja, A. Duque, C. E. N. Ewango, G. A. Fischer, C. Fletcher, J. A. Freund, C. Giardina, S. J. Germain, G. S. Gilbert, Z. Hao, T. Hart, B. C. H. Hau, F. He, A. Hector, R. W. Howe, C. Hsieh, Y. Hu, S. P. Hubbell, F. M. Inman-Narahari, A. Itoh, D. Janík, A. R. Kassim, D. Kenfack, L. Korte, K. Král, A. J. Larson, Y. Li, Y. Lin, S. Liu, S. Lum, K. Ma, J. Makana, Y. Malhi, S. M. McMahon, W. J. McShea, H. R. Memiaghe, X. Mi, M. Morecroft, P. M. Musili, J. A. Myers, V. Novotny, A. de Oliveira, P. Ong, D. A. Orwig, R. Ostertag, G. G. Parker, R. Patankar, R. P. Phillips, G. Reynolds, L. Sack, G. M. Song, S. Su, R. Sukumar, I. Sun, H. S. Suresh, M. E. Swanson, S. Tan, D. W. Thomas, J. Thompson, M. Uriarte, R. Valencia, A. Vicentini, T. Vrška, X. Wang, G. D. Weiblen, A. Wolf, S. Wu, H. Xu, T. Yamakura, S. Yap, J. K. Zimmerman, and A. Kerkhoff. 2018. Global importance of large-diameter trees. Global Ecology and Biogeography 27:849–864.

Mitchell, R. G. 1966. Infestation characteristics of the Balsam woolly aphid in the Pacific Northwest. Research Papers. Pacific Northwestern Forest and Range Experiment Station.

Mitchell, R. G., and P. E. Buffam. 2001. Patterns of Long-Term Balsam Woolly Adelgid Infestations and Effects in Oregon and Washington. Western Journal of Applied Forestry 16:121–126.

Overhulser, David. L., I. R. Ragenovich, M. McWilliams, and E. A. Willhite. 2004. Balsam Woolly Adelgid Occurrence on True Fir in Oregon. Pest Management Report, Oregon Department of Forestry.

Page, G. 1975. Impact of Balsam Woolly Aphid Damage on Fir Stands in Newfoundland. Environment Canada, Forestry Service, Newfoundland Forest Research Centre Information Report N-X-94.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Schooley, H. O., and D. G. Bryant. 1976. The Balsam Woolly Aphid in Newfoundland. Newfoundland Forest Research Centre.

Shore, T. L., and L. Safranyik. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Pacific Forestry Centre.

Skulason, B., O. K. Hansen, I. M. Thomsen, V. Talgø, and U. B. Nielsen. 2017. Damage by *Neonectria neomacrospora* and *Adelges piceae* in provenance trials of subalpine fir (*Abies lasiocarpa*) in Denmark. Forest Pathology 47:e12326.

Varty, I. W. 1956. Adelges Insects of Silver Firs. Forestry Commission Bulletin 26.

CHAPTER 4

CONCLUSION

Since it was first detected in the early twentieth century, BWA has proved to be a damaging and perplexing invasive forest insect. It has caused significant damage and mortality in true fir populations but occurs with a substantial amount of variability in the severity of damage observed. Changes in forest structure, density, and reduced tree species diversity have made subalpine fir stands more susceptible to insect infestations and mortality events and increases in mortality rates have been observed in subalpine fir due to other agents such as bark beetles and climate change. Now well established in northern Utah where subalpine fir is abundant, BWA must be considered a part of the larger subalpine fir "mortality complex."

This study sought to examine the interactions between BWA, host trees, host forests, and abiotic factors. Our results suggest that individual tree characteristics, including DHB and height, are not good predictors of expected BWA-related damage. Stand-level characteristics explained a significant amount of variance observed in BWA-related damage among stands in our plots, the most important of which is related to the structure of subalpine fir stands. Stands with lower structural complexity experienced more severe BWA-related damage. While the temporal limitations of this study likely affected its ability to discern interactions between BWA and other subalpine fir pests, we found that the presence of fir broom rust was associated with less BWA-specific symptoms.

From the characteristics determined to be important predictors of BWA-related damage, a hazard rating model was developed that incorporates stand conditions and climate factors to aid in predicting BWA-related damage and facilitate implementation of management strategies. This three-leveled hazard rating model utilized host structural complexity and autumn precipitation among others as the primary input terms, and additional observations and recommendations were provided to better allocate limited resources in BWA monitoring. Further research is needed to understand the significant drivers of BWA infestations and how patterns of damage and mortality in the newly invaded range in Utah differs from that in the Pacific Northwest. Our study provides a large base of identified relationships and observations to guide future efforts.