

The Role of Abiotic and Biotic Factors in
Douglas-fir Decline in the Western Cascades, Washington

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A thesis

submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington

2017

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Program Authorized to Offer Degree:

Environmental and Forest Sciences

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Abstract

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Washington

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Douglas-fir (*Pseudotsuga menziesii*) dominated forests of the Pacific Northwest are an integral part of the region and provide numerous ecosystem services. They are particularly important in the Cedar River Municipal Watershed (CRMW), Washington, where they provide erosion control and ecosystem buffering for the reservoir, which supplies drinking water to >1.4 million people in the greater Seattle area. Recent records from the CRMW suggest that annual mortality of Douglas-fir has increased in recent years. The Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) and fungal pathogens are key agents of mortality in mature or physiologically stressed Douglas-fir trees, but their contributions to the current rates of mortality in the CRMW is unknown. In this study, I measured relationships between temperature and

Douglas-fir beetle seasonality through development of a phenology model. I then used this model to show how future climate change conditions will be conducive to an expansion of seasonality. Second, I quantified the individual and interacting roles of Douglas-fir beetle; the fungal pathogen, *Armillaria* spp.; and other abiotic and biotic variables as drivers of Douglas-fir mortality in the CRMW. The identified combination of variables could be used to inform managers and help develop adaptive management techniques for at-risk forests.

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ACKNOWLEDGEMENTS

I am extremely grateful for the help of my advisor, Patrick Tobin, who has been endlessly patient with me and helped solve the countless problems that arose during the planning and execution of this project, not to mention editing three theses simultaneously while teaching classes and running a lab. I would also like to thank the other members of my committee, Greg Ettl, Charles Halpern, and Van Kane, who provided a variety of viewpoints and valuable comments throughout my time at UW. My research efforts would have been borderline impossible without the constant help of Amy LaBarge of Seattle Public Utilities, who not only made my work operationally possible within the Cedar River Municipal Watershed, but was also always on the lookout for interesting stands to visit and always making sure everything was running smoothly. Additionally, I owe many “thank-you burritos” to my labmates for their help both in the field and in the lab. I also could not have finished this work without the help of my interns, Jake Betzen, Constance Lin, and Mikaela Balkind. They were always happy to get lost in the woods with me, and were remarkably good at pretending they enjoyed spending hours in the lab counting beetles.

Finally, I would like to thank my family. My parents, Patricia and David, were always infinitely supportive and loved hearing about my work. My sisters, Liz and Audrey, helped push me through the graduate school process and always asked questions to keep me on my toes. Lastly, my fiancé, Nicolas Swaner, deserves special thanks for laughing with me on the good days and being a perfect guiding light on the stressful ones. I could not have done this without him while maintaining my sanity.

Chapter 1. AN INTRODUCTION TO RESEARCH ON DOUGLAS-FIR BEETLE (*DENDROCTONUS PSEUDOTSUGAE* HOPKINS) POPULATION DYNAMICS AND DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII*) MORTALITY.

The Douglas-fir (*Pseudotsuga menziesii*) dominated forests of the Pacific Northwest are an integral part of the region and provide numerous ecosystem services. These services are particularly important in the Cedar River Municipal Watershed (CRMW), Washington, which provides critical ecosystem services by supplying clean drinking water to >1.4 million people in the greater Seattle area (Mollot et al. 2007). Recent observations at the CRMW suggest that annual mortality of Douglas-fir is considerably higher than historical averages in similar mature forests (<5% per year; (Bible 2001, Larson et al. 2008). This could be due to changing environmental that increase tree physiological stress, thus rendering trees more susceptible to attack from biotic agents. The Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) and fungal pathogens are key agents of mortality in mature or physiologically-stressed Douglas-fir trees, but their contributions to current elevated rates of mortality in the CRMW is unknown.

The Douglas-fir beetle, in addition to its role as an agent of mortality in second-growth Douglas-fir dominated forests in the Pacific Northwest, also plays an important role in stand diversification and succession (Lessard and Schmid 1990). Historically, the species has been considered univoltine, with a single generation of adults, and larvae that overwinter and emerge in spring under favorable temperature conditions (Johnsey et al. 1965, Hood et al. 2007). However, the seasonality of Douglas-fir beetle is understudied, especially in western Washington

forests. The first objective of my thesis, presented in Chapter 2, is to characterize Douglas-fir beetle phenology in western Washington and to develop a degree-day model to predict the occurrence of adults. I used seven years of field-collected beetle-trap data, and related these data to local temperature records to develop a degree-day-based phenology model. I then extended the predictions of this model under the B1 climate change scenario (Intergovernmental Panel on Climate Change, 2014) to project how future climate change would alter Douglas-fir beetle seasonality and its potential consequences for Douglas-fir mortality.

The second objective of my thesis, presented in Chapter 3, is to quantify the individual and interacting roles of the Douglas-fir beetle and the fungal pathogen, *Armillaria* spp., as well as other abiotic and biotic stand metrics, as drivers of Douglas-fir mortality in the CRMW. Using 2 years of field data, I analyzed the relationships between multiple abiotic and biotic factors and (1) presence of stand-level root-rot infection from *Armillaria* spp., (2) presence of Douglas-fir beetle attacks, and (3) Douglas-fir mortality. These relationships should be useful in developing adaptive management techniques for the CRMW and other at-risk forests within western Washington.

Climate change is likely to exacerbate stress to the Douglas-fir dominated forests of western Washington, which could lead to increased attacks by biotic agents, and increased mortality (Van Mantgem et al. 2009, Allen et al. 2010, Intergovernmental Panel on Climate Change 2014). My research suggests that the seasonality of Douglas-fir beetle will likely expand in response to climate change with important consequences for host trees with reduced vigor that are more susceptible to insect attack. This may be particularly evident in low elevation forests dominated by Douglas-fir that provide sufficient host material to support the development of Douglas-fir outbreaks. Widespread Douglas-fir mortality could lead to shifts in forest structure at

faster rates than expected under historical conditions, which puts essential ecosystem services at risk.

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Chapter 2. PHENOLOGY OF THE DOUGLAS-FIR BEETLE, *DENDROCTONUS PSEUDOTSUGAE* HOPKINS (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE), IN WESTERN WASHINGTON

2.1 ABSTRACT

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is a primary agent of mortality in Douglas-fir (*Pseudotsuga menziesii*) dominated forests of the Pacific Northwest. The Douglas-fir beetle plays an important role in both vigorous and physiologically stressed stands. Its phenology in western Washington is understudied, which limits our ability to characterize its current seasonality or how it could change under future climatic conditions. I used trapping data collected over 8 years in western Washington to develop a phenological model of adult beetle flight. I then extended this model to better understand the potential effects of climate change on beetle seasonality by considering the B1 climate change scenario (+1.7 °C; Intergovernmental Panel on Climate Change, 2014) at my study sites. Empirical data indicate that beetle flight at the beginning of spring is significantly correlated to mean ambient temperature, and that this relationship becomes progressively less significant later in the season. The phenological model suggests that higher temperatures during early spring will allow for temporal expansion of beetle activity. This work should help facilitate improvements to current sampling efforts and provide a framework for understanding Douglas-fir beetle seasonality under future climatic conditions.

2.2 INTRODUCTION

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is an ecological and economic pest of its host tree, Douglas-fir. It is a driver of successional processes in younger and mature Pacific Northwestern forests (Lessard and Schmid 1990), spurring long-term changes in canopy and understory diversity (Raffa et al. 2008). The species preferentially selects larger-diameter individuals, likely due to limitations associated with anatomical size and energetic rewards (Powers et al. 1999). The species has historically been considered univoltine (Johnsey et al. 1965, Hood et al. 2007), although there is disagreement on whether its behavior is facultative or obligatory (Ryan 1959, Wood 1982, Bentz et al. 2010). Individuals overwinter either as late instars or adults. Those overwintering as adults are the first to emerge and reproduce in mid- to late spring, after which females oviposit into suitable host trees. Late-summer attacks are most likely initiated by individuals that overwintered as larvae in the previous year, and continued their development in the subsequent spring and summer (Lessard and Schmid 1990, Dodds 2003, Li 2014).

Several pheromones are used to signal conspecifics about mating availability and host viability. Known pheromones are emitted exclusively by females (trans-verbenol, verbenone, and 3,2-MCH-ol) or both males and females (frontalin, 3,2-MCH, and 3,3-MCH). Both males and females identify hosts by the kairomones they emit (camphene and α -pinene) and the tree-stress signal ethanol (Wood 1982, Lingren 1983, Lingren et al. 2012). In combination, these volatile compounds act as packets of information that can induce beetle mating and colonization of hosts. After mating, adult females create vertical egg galleries between the bark and cambium of host trees and oviposit up to 60 eggs (Thong and Webster 1975). Larvae hatch within 1-3 weeks after egg laying and feed within the phloem, tunneling laterally through the living tissue and disrupting

the flow of photosynthates (Negrón et al. 2001). An individual attack within a single tree is unlikely to be successful or to affect host vigor; however, larger-scale infestations can cause mortality. In general, healthy trees are resilient against colonization attempts by Douglas-fir beetles, especially when surrounded by other non-immunosuppressed host trees (Li 2014).

The Douglas-fir first-line-of-defense against Douglas-fir beetle is the exudation of oleoresin through resin canals during an attempted colonization event. Beetles are repelled when exposed to the substance and can be killed if trapped within it (Rudinsky 1966, Keeling and Bohlmann 2006). If colonization and egg laying is successful, the host tree can induce increased production or concentration of additional toxic compounds in necrotic tissue surrounding the gallery to kill the eggs and larvae within (Christiansen et al. 1987, Raffa and Berryman 1987, Mumm and Hilker 2006). Pitch exudation as an effective response to sub-periderm invasion is limited by tree vigor, however. Physical anatomy of the adult exoskeleton allows actively burrowing individuals to push out frass as well as small amounts of pitch. Trees experiencing physiological stress including drought, shading, fungal-pathogen infection, or fire, ice or wind damage, have difficulty diverting enough photosynthate to mount this immune response (Furniss 1965, Furniss et al. 1979, Oliver and Larson 1996, Powers et al. 1999, Keeling and Bohlmann 2006, Fettig et al. 2007). This is especially a problem in stands experiencing multiple stressors, including windthrow, pathogens, and drought (Wright and Lauterbach 1958, Christiansen et al. 1987, Ross and Daterman 1995, 1997, Powers et al. 1999, Negrón et al. 2001, Keeling and Bohlmann 2006, Bansal et al. 2016).

Outbreaks of Douglas-fir beetles are often temporally associated with significant windthrow in Douglas-fir forests (Christiansen et al. 1987, Powers et al. 1999, Mitchell 2000). Similarly, fungal pathogens, specifically *Phellinus* spp. and *Armillaria* spp., are additional sources

of biotic stress (breaking down living tissue; Hansen and Goheen 2000) and can promote beetle attacks. Finally, drought stress can decrease stand vigor at landscape to regional scales (Bansal et al. 2016). Forests experiencing drought, and those in topographically dryer environments, have stronger associations with beetle outbreaks (Powers et al. 1999, Fettig et al. 2007). Douglas-fir beetles only attack living trees, but trees that have been damaged or uprooted by windstorms, have an ongoing pathogen infection, or are experiencing drought, can be attacked. Once an infestation has been initiated following a stand-scale disturbance, the beetle population can increase to where attack density will begin to kill otherwise non-immunosuppressed trees on the periphery of the infestation area; this may occur within 1-3 years of the initiating disturbance (Wood 1982, Ross and Daterman 1995). Beetle populations are not evenly distributed through forests, but are concentrated in these areas of ongoing infestation – even in outbreak years with abnormally high population levels (Negrón et al. 2001, Dodds 2003). In contrast, beetles maintain low-density populations in stands not experiencing environmental or biological stressors, reproducing within few individually damaged or otherwise compromised host trees (Powers et al. 1999).

A future abiotic stressor in forest ecosystems is the projected increase in surface temperature. Even conservative climate-change scenarios project an increase of at least 1.7°C by 2100 (Intergovernmental Panel on Climate Change, 2014). In addition to a general warming trend, climate change could result in more frequent sub- or supra-optimal precipitation or temperature events, which could be problematic for species not adapted to this variability (Casola et al. 2005, Salathe et al. 2007, Mote and Salathe 2010). With climate change presenting the possibility of stressful disturbances becoming more frequent, climate models for the Pacific Northwest suggest that climate change may already be one of the many factors at play (Bale et al. 2002, Raffa et al. 2008, Bentz et al. 2010). Understanding Douglas-fir beetle population dynamics and the conditions

that promote increases in population density is an important step in the development of management practices. An improved understanding of current and future population dynamics under changing climatic conditions, could furthermore enhance management practices. For example, others have examined the phenology of a congener, the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) (Bentz et al. 1991, Logan and Bentz 1999, Régnière and Bentz 2007, Raffa et al. 2008). Recent analyses of its range expansion and increased intensity and frequency of outbreaks suggest that *Dendroctonus* spp. are able to take advantage of increasing average temperatures, to the detriment of forest health (Carroll et al. 2003, Hicke et al. 2006, Sambaraju et al. 2012). These studies have contributed to a better understanding of their outbreak dynamics, and suggest best-management practices to adapt to these dynamics, in what may be novel, climate change-driven phenology.

A prior study of Douglas-fir beetles described the relationships between adult fat content and larval rearing temperature regime (Atkins 1967). However, extending this knowledge into a broader understanding of its seasonality remains understudied. Areas of unusually intense infestations are associated with adjacent infestations (Dodds 2003), although the temporal and spatial scale over which outbreaks erupt is currently not well known. The geographic range of the Douglas-fir beetle lies within temperate North America and, as a result, it is largely regarded as undergoing obligate diapause. However, past work has shown that this diapause requirement can be experimentally manipulated, suggesting that diapause could be facultative (Ryan 1959). Due to their association with older or otherwise immune-suppressed trees, Douglas-fir beetles are a strong indicator of overall forest stand resilience and stability, and are used by forest managers to monitor the success of their practices in relation to management goals (Powers et al. 1999, Fettig et al. 2007).

While the general relationship between temperature and insect development is well established (Mellanby 1939, Bullock 1955, Bale et al. 2002, Sambaraju et al. 2012), relationships can vary considerably among species, and currently are not well understood for Douglas-fir beetle. Degree-day models for other insect species have been used to link early-flight seasonal dynamics with late-flight seasonal dynamics (Hansen et al. 2001a, Régnière and Bentz 2007, Bentz et al. 2010). In Douglas-fir beetle, it is assumed that overwintering adults, having undergone metamorphosis during the previous summer and fall, emerge fully developed and likely initiate flight in spring when temperatures exceed some minimum or a degree-day threshold. In contrast, overwintering larvae still require a specific duration of degree days to complete development in the following spring and summer prior to emerging as adults later in the year (Ryan 1959). Because insect developmental rate depends on temperature, degree-day models are a useful tool to predict insect phenology (Allen 1976, Pruess 1983, Hagstrum and Milliken 1988). Although the minimum developmental threshold is currently unknown in Douglas-fir beetles, data provided by Atkins (1967) could be used to estimate this threshold, from which a degree-day model can be developed.

In this paper, I sought to model the seasonality of Douglas-fir beetle flight and to develop a degree-day model. I then use this degree-day model to link early-flight seasonal dynamics with late-flight seasonal dynamics. Lastly, I examine observed patterns of flight relative to the B1 climate change scenario in which mean temperatures are increased by 1.7°C.

2.3 MATERIALS AND METHODS

Sampling Locations

Douglas-fir beetle populations were monitored at the Cedar River Municipal Watershed (CRMW), North Bend, WA, in 2005, and again from 2007 to 2010, using Lindgren funnel traps.

However, most trapping was implemented within a period during which Douglas-fir bark beetles were historically expected to already be active. Consequently, it is not always possible to infer from these data, when initial spring flight began or how long beetles remained active in flight in the fall. Increasing the temporal period of sampling, as well as the frequency at which traps are monitored, facilitates a more robust analysis of Douglas-fir beetle seasonality. In addition, enlarging the spatial scale (extent) over which traps are monitored allows for a spatially more robust phenological model. In this study, I increased the number of trapping areas within the CRMW and the frequency at which traps were checked. I also deployed traps at two additional sites: the University of Washington Center for Sustainable Forestry at Pack Experimental Forest (Eatonville, WA), ~75 km south of the CRMW, and the University of Washington Lee Memorial Forest (Snohomish, WA), ~53 km north of the CRMW (Fig. 2.1). I collected data from 2015-2017 at the CRMW and Pack Experimental Forest, and from 2016-2017 at Lee Memorial Forest.

The CRMW is a controlled-access forest reserve covering roughly 364 km², including a large water reservoir. This reservoir exists as the source of drinking water for ~1.4 million people in the greater Seattle area. The CRMW contains a Douglas-fir (*Pseudotsuga menziesii*) dominated second-growth forests; most stands are roughly 80 years old. Pack Experimental Forest is a 17.4 km² public-access working forest containing both active logging areas and numerous forestry study sites, with stands ranging in age from newly clear-cut to old-growth (~800 years). Lee Memorial Forest is 0.64 km² of public-access, second-growth Douglas-fir forest surrounded by suburban development. To complement trap collection data, temperatures were recorded hourly using HOBO data loggers (Onset Computer Corp., Bourne, MA) before and throughout the sampling period. Historical temperature data, for use with trapping data from the CRMW in 2005 and 2007-2010, were acquired from National Centers for Environmental Information (2017).

Sampling Schedule

At each study site, I deployed 12-unit multiple funnel traps (Lingren 1983, Ross and Daterman 1995). Traps were deployed in pairs at each sampling locations (i.e., 2 traps per sampling location) within each study site. Traps were baited with semiochemical lures comprising three distinct elements. A 6-ml low-release packet of ethanol was attached to the top funnel, chemically simulating a physiologically stressed Douglas-fir (Ross and Daterman 1995, Kelsey and Joseph 2001, Kelsey et al. 2016). A packet containing 2745 μ l of frontalin (1,5-dimethyl-6,8-dioxo-[3,2,1]-bicyclooctane) and 250 μ l of seudenol (3-methyl-2-cyclohexen-1-ol) was hung on the 6th funnel, acting as a Scolytinae aggregation pheromone (Ross and Daterman 1995, 1997, Lingren et al. 2012). A 15 ml packet of Douglas-fir kairomone blend was hung on the 11th funnel, acting as a host identifier (Kelsey and Joseph 2001) (Fig. 2.2).

Historical trapping data from the CRMW (2005, 2007-2010) varied yearly, ranging from 5 to 11 sampling locations. Traps were typically checked every 1-2 weeks from the last week of April until late July or early August. I deployed traps at the CRMW at 11, 12, and 9 sampling locations in 2015, 2016, and 2017, respectively, selecting from previously used sampling locations. At Pack Experimental Forest, I deployed traps at 12, 6, and 5 sampling locations in 2015, 2016, and 2017, respectively. Trapping effort after 2015 was reduced due to logging activity and allowed for trapping at Lee Memorial Forest. I deployed traps at 3 sampling locations at Lee Memorial Forest in 2016 and 2017. Trap locations in the CRMW were chosen based on historical trap locations, while sites in all additional sampling areas were chosen based on proximity to known active Douglas-fir beetle infestations, ease of access, and to maximize spatial coverage. Traps within each pair at all sampling locations were ~100 m apart.

In 2015, trap set-up was delayed until early July due to problems associated with the lure supplier. Once deployed, traps were checked weekly at Pack Forest and every 2 weeks at the CRMW until the week of October 5. In 2016, traps were deployed at all sites during the week of March 20, and checked weekly until the week of September 26th. In addition, three pairs of traps were left at the CRMW to measure late season beetle flight until 12 December 2016. In 2017, traps at all three sites were deployed between 9 March and 13 March 13, and were checked weekly until the week of July 31.

Analyses

I first measured the relationship between temperature and beetle flight activity. Weekly beetle counts from all trapping data were transformed using $\log_{10}(y + 1)$ to normalize the distribution. Mean daily temperatures were computed from hourly temperature data. I then measured the Pearson Correlation Coefficient between weekly beetle counts and temperature. These correlation values were then plotted along their respective calendar day of data collection, from which I sought a date that separates early season (e.g., overwintering adults) from late season (e.g., overwintering larvae) beetle flight. I did this based upon the assumption that overwintering adults only require sufficient temperatures to initiate flight and thus relatively little degree day accumulation, which is in contrast to the degree day requirements of overwintering larvae. Thus, I hypothesized that there would be a stronger correlation between weekly average temperature and the number of trapped beetles during early-season flight than during late-season flight.

Based on the delineation of early-season beetle flight, I then sought to develop a phenology model for initial beetle flight. I used linear regression of temperature-developmental data from Atkins (1967) to estimate a minimum base temperature threshold, which was estimated at 4.3°C.

Using daily maximum and minimum temperature data (either from National Centers for Environmental Information or from our deployed HOBO units), I estimated daily degree day accumulation, based upon the minimum base threshold estimate of 4.3°C, using the sine wave method (Allen 1976, Tobin et al. 2001). I then modeled the cumulative proportion of early season beetle flight (P) as a function of accumulated degree days (DD) according to:

$$P = \exp(-\exp(-a \times DD + b)) , \quad (1)$$

in which a is a parameter representing the rate of increase to the optimal temperature and b is a parameter representing the lag. I used nonlinear regression and the Marquardt algorithm for convergence (Marquardt, 1963).

Lastly, I estimated potential fluctuations in the seasonality of the Douglas-fir beetle under the B1 climate change scenario. Daily minimum and maximum temperature values for all sampling years at the CRMW were increased by 1.7°C (Intergovernmental Panel on Climate Change, 2014), after which I estimated daily degree day accumulations using the same minimum base threshold estimate of 4.3°C and the sine wave method. These climate change-derived degree day values were then linked with beetle flight data to compare Douglas-fir beetle seasonality.

2.4 RESULTS

We observed similar general patterns of Douglas-fir beetle flight activity across years, although there were differences in the timing of initial flight (Fig. 2.3). For example, the timing of initial flight varied by 26 days between the “warmest” and “coolest” year during the sampling period. The greatest beetle flight activity occurred in early spring, with peak means at the CRMW

ranging between 1,345 (2008, Fig. 2.4 & 2.5) and 185,188 (2016, Fig. 2.4 & 2.6) beetles. Successively smaller peaks were observed over the course of the summer, ranging from 0 (multiple years, all sites, Fig. 2.4) to 16,932 beetles (2017, CRMW, Fig. 2.4). Generally, no beetles were trapped after calendar day 261.

In tests of significance of correlation values between log₁₀-transformed weekly beetle data and weekly mean temperature, I observed two separate and significantly different temporal groups of beetle flight (Fig. 2.7). Calendar day 157 bisects the correlation values into early flight (pre-calendar day 157), in which I measured a significant correlation between beetle counts and temperature, and late flight (post-calendar day 157), in which correlation coefficients were not significant (Fig. 2.7). These two temporal subsets also had dissimilar relationships with temperature: beetle activity in the early flight subset had a positive and statistically significant relationship with temperature ($\rho=0.74$, $P<0.01$), while beetle activity in the late flight subset had a non-significant relationship with temperature ($\rho=0.19$, $P=0.10$; Fig. 2.8).

Based on the correlations between weekly beetle count and mean temperatures, I considered the ‘initial flight’ period as data collected from the onset of flight until day 157. The cumulative proportion of beetle flight during initial flight as a function of degree day accumulation is shown in Figure 2.9. I used the nonlinear regression model (Eq. 1) to estimate the degree-day accumulation for specific percentiles of beetle flight (Table 2.1). Peak beetle flight (i.e., 50th percentile) is reached at 344.5 degree-days, and the cumulative proportion of beetle activity becomes asymptotic at ~ 801.6 degree-days (Fig. 2.9). Degree day accumulation estimates then were associated with their respective calendar days and beetle flight proportions (Fig. 2.10).

Based on mean daily degree-day accumulation using temperature data from the CRMW over the sampled years, I projected changes in daily degree day accumulation and the

corresponding shifts in Douglas-fir beetle seasonality when assuming the B1 climate change scenario (Table 2.1). Under the B1 scenario, 5, 50, and 95% cumulative flight activity is projected at days 59.7, 125, and 175, respectively. This resulted in seasonality being shifted by 21-27 days (Fig. 2.10, Table 2.1). 2005 and 2016 temperatures were both above the B1 scenario after calendar day 50, while all other years were below it.

2.5 DISCUSSION

An analysis of Douglas-fir beetle flight data reveals many time- and temperature-related patterns. The flight peak frequency and timing of beetle flight seasonality vary considerably both among and within years, and calendar day flight peaks frequently overlapped among years (Fig. 2.3). The end of flight was also fairly consistent across years and sites.

The largest peaks in beetle flight typically occurred in early spring. Winter temperatures are well known to synchronize insect emergence in the following spring (Bjørnstad et al. 2016). Insects that overwinter as adults often require no to few degree days to emerge and can initiate flight as soon as temperatures are sufficiently warm to engage in flight. Successively smaller flight peaks after calendar day 157, and especially between days 170 and 240, likely represent the adult emergence of individuals that overwintered as larvae given the absence of a significant correlation with mean weekly temperatures (Fig. 2.7 and 2.8). The smaller peaks during the late season relative to the early season could reflect larval and pupal mortality, as well as a tendency for adult emergence to become less synchronized due to differential rates of development (Bjørnstad et al. 2016). It is also possible that a greater fraction of the population overwinters as adults. Regardless, a tendency for adults to emerge earlier in spring would lead to earlier oviposition. A direct consequence of earlier emergence could be that a greater fraction of individuals will overwinter as adults leading to an increase in spring attacks on Douglas-fir. Additionally, larvae developing over

the course of summer in warmer conditions would develop faster. Earlier spring flight is likely preferred not just for greater availability of mates and first choice of host trees, but also as a means of ensuring faster development of progeny in ideal phloem movement conditions without the risk of larval mortality due to extreme cold events (Bentz et al. 1991, Régnière and Bentz 2007). Because spring flight capacity is more limited by adult lipid content than summer flight (Atkins 1967, Thompson and Bennett 1971, Williams and Robertson 2008), greater beetle density in spring could reduce energy expended in locating mates, and synchronize mass attacks on host trees.

Flight activity at the beginning of the year is initially significantly positively correlated with weekly mean temperature, and the significance of this relationship declines through the year (Fig. 2.7 & 2.8). This could reflect the decreasing effects of initial flight temperature thresholds (critical to overwintering adults) and the switch to degree-day accumulation needed to complete development in overwintering larvae. Although temperature is important to developing larvae, cumulative heating is required over several weeks to months, which reduces the importance of a mean temperature during an individual week (Pruess 1983, Anderbrant 1986, Ayres et al. 2001, Hansen et al. 2001b, a). Moreover, temperatures in summer are consistently over the minimum development temperature threshold (4.3°C), and thus degree days are being accumulated each week over the summer. By temporally subsetting the season into early and later flight, I can better estimate initial flight as well as late-season flight to help support Douglas-fir beetle management programs.

Historically, many *Dendroctonus* species were thought to either require diapause or never require diapause (Safranyik and Whitney 1985, Hansen et al. 2001a). However, recent studies have suggested the possibility of facultative diapause. For example, the spruce beetle, *Dendroctonus rufipennis* Kirby (Coleoptera: Curculionidae: Scolytinae), was thought to undergo obligate

diapause, but recent efforts have shown that it can be reared without it (Hansen et al. 2001a, b). Mountain pine beetle is thought to undergo diapause only when exposed to extreme cold winter conditions, suggesting facultative diapause (Hicke et al. 2006, Régnière and Bentz 2007, Lester and Irwin 2012). Pest management guidelines for Douglas-fir beetle largely consider the species to exhibit obligatory diapause (Schmitz and Gibson 1996, Kegley 2011); yet, individuals have been reared experimentally without diapause (Ryan 1959). This suggests that Douglas-fir beetle could undergo facultative diapause depending on weather conditions. Considering how climate change is broadening the geographic range and intensity of outbreaks of the congeneric mountain pine beetle (Bale et al. 2002, Bentz et al. 2010), the possibility of a temporal expansion of Douglas-fir beetle seasonality in future climate conditions warrants additional study (Fig. 2.10 & 2.11). The unusually early flights of 2005 and 2016 suggest that climate change will promote significantly earlier emergence than the norm (Bale et al. 2002). Furthermore, population success is likely to increase as host vigor declines under warmer and drier summer conditions (Bentz et al. 2010).

Conservative climate-change estimates place average global temperatures increasing by at least 1.7°C over the next century (Intergovernmental Panel on Climate Change 2014). The potential for an additional generation of beetles due to facultative diapause may pose a challenge to management. Moreover, current climate patterns in western Washington are characterized by reduced precipitation in summer and early autumn relative to winter and spring; for example, 73% of the precipitation at the CRMW occurs from November to the following May (National Centers for Environmental Information 2017). This skewed seasonal weather pattern already puts Douglas-fir under water stress and could make them more vulnerable to attack from a second generation of beetles under future climate warming conditions. This could either exacerbate current mortality trends, or actually be a component of elevated rates of mortality in Douglas-fir due to Douglas-fir

beetle (Case and Peterson 2005, Hicke et al. 2016). In fact, beetle-driven mortality events over the last decade have rivaled or surpassed those of forest fires in both geographic range and overall number of successful tree mortality events (Hicke et al. 2016, Logan et al. 2017). The possibility of these trends expanding to the western Cascades region is uncertain. Given projections for future beetle phenology (Fig. 2.10), however, the potential certainly exists.

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Chapter 3. THE CONTRIBUTION OF BIOTIC AND ABIOTIC FACTORS TO DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII*) MORTALITY IN WESTERN WASHINGTON FORESTS

3.1 ABSTRACT

Lowland second-growth forests in the Puget Sound region are largely dominated by Douglas-fir. The Cedar River Municipal Watershed (CRMW), a controlled-access and mostly second-growth forest containing the source and reservoir of drinking water for 1.4 million people, is managed for potential impacts to water quality. Unusually high mortality of Douglas-fir throughout the watershed has presented the opportunity to identify the biotic and abiotic factors associated with this phenomenon. I used a series of fixed-radius plots to measure a variety of forest metrics across a Douglas-fir mortality gradient throughout the CRMW. I then used LASSO regression analyses to identify which forest metrics were related to stand-level mortality, Douglas-fir bark beetle (*Dendroctonus pseudotsugae* Hopkins) activity, and root rot (*Armillaria* spp.) infection. Results suggest that stand-level Douglas-fir mortality is affected by biotic and abiotic factors, including beetle activity and root rot. Furthermore, these factors could be exacerbated by prolonged summer drought, which is common to this region. This study should assist forest managers in identifying at-risk stands and support the development of targeted management practices.

3.2 INTRODUCTION

Douglas-fir (*Pseudotsuga menziesii*) dominated forests of the Pacific Northwest are an integral part of the regional ecosphere, providing ecological buffering in the hydrological systems of western watersheds (Mollot et al. 2007). The municipal water supplies for many northwestern cities are sourced from artificial reservoirs surrounded by these forests, and their roles in water filtration and retention are fundamental in maintaining high-quality drinking water (Hansen and Ongerth 1991, Postel and Thompson 2005). The ability of these forests to serve as buffers may rely, in part, on the ability of managers to react to disturbance events and the cascade of successional responses that typically follow.

Historical annual mortality of Douglas-fir in mature stands in the Pacific Northwest has typically been 1-5% (Bible 2001, Larson et al. 2008), yet many mature stands in the Cedar River Municipal Watershed (CRMW) are exhibiting annual mortality rates of 30-50% (A. LaBarge, Seattle Public Utilities, personal observations). To examine the underlying processes that may be driving what appears to be unusually high mortality rates in the CRMW, a baseline for expected forest developmental processes in similarly maturing Douglas-fir stands must first be considered. Mortality in stands dominated by younger Douglas-fir tends to be competition-driven, as smaller, suppressed individuals ($DBH \leq 25$ cm) die, and larger, more dominant individuals persist (Franklin et al. 2002b). Mortality in older stands is typically lower and tends to be driven by density-independent factors (He and Duncan 2000, Bible 2001, Franklin et al. 2002b), processes unrelated to the local density of trees. In Douglas-fir forests, these include root rots (*Armillaria* spp., among others), attack by Douglas-fir beetles (*Dendroctonus pseudotsugae* Hopkins), mechanical disturbances (wind snap or windthrow), and interactions among these (Powers et al. 1999, Hansen and Goheen 2000, Franklin et al. 2002b, Fettig et al. 2007). The transition from competition-

agent-based causes of mortality typically occurs over 100-150 years in the PNW (Franklin et al. 2002a), although it has not been studied explicitly in older second-growth forests of the CRMW. A primary concern in the CRMW is that current increases in mortality may indicate stand conditions that are particularly susceptible to agent-based mortality, which could be further exacerbated by future climate conditions.

Forests are dynamic ecosystems, and as such they vary in their patterns of growth and mortality as they age. Young, post-stem exclusion forests in the western Cascades tend to have low tree diversity, increasing the risk of attack by biotic agents (Spies 1996, Franklin et al. 2002b, Reilly and Spies 2016). Mortality rates in early-middle age class stands experience non-annual “waves of mortality” throughout the stages of development, when annual mortality rates can reach 10-30% due to weather and biotic agent-based events (Oliver and Larson 1990). This process is notably distinct from the conditions in the CRMW, as mortality in these situations typically returns to its lower ambient mortality once the disturbance has passed (Bible 2001).

The Douglas-fir beetle is a key cause of mortality in mature, physiologically stressed, very recently windthrown, or fire-damaged Douglas-fir (Lessard and Schmid 1990). After mating, adult females create egg galleries between the bark and cambium of host trees, and oviposit up to 50 eggs (Thong and Webster 1975). Larvae feed within the phloem, and in heavy infestations, disrupt the flow of photosynthates enough to cause mortality (Schmitz and Gibson 1996, Li 2014). Identifying the stand conditions that facilitate large-scale Douglas-fir beetle-driven mortality events is an important step in developing management practices that can reduce the potential for mortality and its ecological consequences, and facilitate the post-disturbance recovery process. Due to their association with older or otherwise immunosuppressed trees, the Douglas-fir beetle is a strong indicator of overall forest resilience and stability, is are used by forest managers to monitor

the success of their practices in relation to management goals (Powers et al. 1999, Fettig et al. 2007).

Individual beetle-infested Douglas-fir in the CRMW are not randomly distributed in the CRMW, but rather are clustered in spatially contiguous stands, often over large areas. This spatial clustering is often indicative of agent-based causes of mortality, rather than abiotic stressors (Fettig et al. 2007). The Douglas-fir beetle is one such potential agent in the heightened mortality of Douglas-fir in the CRMW because it has recently been observed in high numbers (Fig. 3.1). Trees in the vicinity of a bark beetle infestation are known to be prone to infestation. However, already stressed trees are considerably more vulnerable to Douglas-fir beetles (Furniss 1965, Bentz et al. 2010, Hicke et al. 2016). A beetle infestation is typically one of the final life events in Douglas-fir, and likely occurs as a consequence of physiological stress rather than a systemic instigator of mortality (Shore et al. 1999). Trees within the CRMW may be experiencing multiple stressors simultaneously, which provide conditions conducive to biotic agent-based mortality.

A variety of stressors are known to be associated with prior or subsequent Douglas-fir beetle infestations. Wind damage is a known abiotic stressor of Douglas-fir and has a strong temporal association with subsequent Douglas-fir beetle outbreaks. Douglas-fir beetles only attack living trees, but trees that have been damaged or uprooted by windstorms and remain alive can be attacked (Powers et al. 1999, Mitchell 2000). Drought stress is also a known contributor to decreased stand vigor both at the regional and landscape scale (Christiansen et al. 1987, Mildrexler et al. 2015, Bansal et al. 2016). Forests experiencing regional drought, as well as stands in locally dryer locations, have stronger associations with beetle outbreaks or episodes of stand-level mortality (Christiansen et al. 1987, Powers et al. 1999, Fettig et al. 2007, Cohen et al. 2016). With climate change presenting the possibility of these disturbances becoming regular events, recent

regional climate trends suggest that climate change may already be one of the many factors at play (Bentz et al. 2010, Mildrexler et al. 2015, Cohen et al. 2016).

The root-rot fungal pathogen, *Armillaria* spp., is associated with Douglas-fir beetle infestations and abiotic factor-driven Douglas-fir mortality (Hansen and Goheen 2000). It is a known driver of forest species diversification and succession, but also causes significant economic losses (Morrison and Mallett 1996). Fungal mycelia spread slowly through root-to-root contact or through soil rhizomorphs among preferred conifer species. Thus, rates of infection and mortality due to *Armillaria* spp. are higher in denser and less diverse stands (Morrison and Mallett 1996, Cruickshank et al. 1997, He and Duncan 2000, Morrison et al. 2001, Baleshta et al. 2005, Cruickshank et al. 2009). Infection by *Armillaria* spp. can stunt both vertical and lateral growth, limiting basal area increases due to stress-induced shifts in energetic resource partitioning regardless of overall pre-infection tree vigor (Morrison and Mallett 1996, Rosso and Hansen 1998, Hansen and Goheen 2000, Cruickshank et al. 2009). Stands that have previously undergone pre-commercial thinning or clear-cut logging also have higher incidence of infection, as the mycelia can readily use stumps as both a food resource and as a root-to-root bridge to adjacent uninfected trees (Hansen 1979, Bloomberg and Morrison 1989, Van Der Kamp 1995, Morrison and Mallett 1996, Cruickshank et al. 1997). Together, the spatial-spread behavior and stand logging history are responsible for the uneven and clumped distribution typical of northwest forest infection areas (Van Der Kamp 1995). The physiological stress induced by infection may also contribute to reductions in volatile terpene production, making individual affected trees more vulnerable to bark beetle attack. Affected stands with large-scale root-rot infections are also more vulnerable to localized beetle outbreaks and consequent mortality (Nebeker et al. 1995).

The CRMW has established a habitat conservation plan (HCP) to outline the restoration and management of its various ecotypes (LaBarge 2017). Considering the erosion control and water-quality management goals for the drinking water reservoir within the CRMW, identifying the drivers of unusually high mortality of a dominant tree species in the surrounding forest will help inform managers on how best to target their management practices for both the reservoir and the HCP. In this paper, I sought to identify the biotic and abiotic variables associated with the observed increased mortality of Douglas-fir within the CRMW.

3.3 MATERIALS AND METHODS

Sampling Locations

I conducted this study at the CRMW in North Bend, WA, in 2016 and 2017. The CRMW is a controlled-access forest reserve covering roughly 364 km². It includes a large reservoir with a surface area of ~7 km² that serves as the source of drinking water for ~1.4 million people in the greater Seattle area. A majority of the CRMW is covered by low-elevation Douglas-fir dominated forest. Most stands are ~80 year-old second growth, although some are considerably older (> 500 years) and more diverse, particularly those at higher elevations (> 1,000 m).

To identify the biotic and abiotic factors associated with increasing Douglas-fir mortality in the CRMW, I sampled affected and unaffected stands across a broad range of topographic, hydrological, and ecological gradients. To structure my sampling, I selected from among 110 permanent sample plots (PSPs), 1/5th acre in area, that are measured every ten years to track forest development (Fig. 3.2A). Standard measurements made in these plots include diameter at breast height (DBH), trees status (live, dead), and trees per acre (TPA). I randomly selected a subset of

PSPs for intensive sampling, stratified into three groups based on plot proximity to areas of known mortality as determined from aerial surveys (Fig. 3.2B).

Aerial survey data were taken in summer 2015 by the Washington Department of Natural Resources Region 6 (1980-2016) to identify areas of likely Douglas-fir mortality across the region, including the CRMW. I assigned each of the 110 PSPs as belonging to one of three mortality classes: (1) high mortality, ≤ 150 m from a mortality area; (2) medium mortality, 150 to 1,000 m from a mortality area; and (3) low mortality, $\geq 1,000$ m from a mortality area (Fig. 3.2B). Before selection from among these plots, several were eliminated because they were not easily accessible. From the remaining PSPs, six were randomly selected from each mortality group for a total of 18 study sites.

Plot Layout and Sampling Schedule

At each selected PSP, I established an additional eight 1/10th acre subplots, positioned in pairs aligned along the four cardinal directions (N, S, E, and W) at 50 and 100 m from the border of the PSP (Fig. 3.3). To maintain consistency in plot size, I also reduced the original PSP plot to 1/10th acre. Thus, at each of the 18 study sites, I collected data from nine 1/10th acre plots. Sampling was conducted between 30 June and 30 August, 2016, and between 21 June and 12 July, 2017. To compliment field data, topographical data was derived from digital elevation models (DEM) in ArcGIS obtained from the United States Geological Survey (2015).

Field Data Collection

In 2016, I collected data on all tree species in all plots and additional data specific to Douglas-fir. For each stem >5 cm DBH I recorded the species and measured the diameter. For

Douglas-fir, I also recorded (1) relative crown thinning class (high, >66%; medium, 33-66%; low, <33%; or none); (2) mortality status (living; 0 = numerous dead needles; 1 = no needles, many smaller branches present; and 2+ = larger branches missing), (3) presence or absence of Douglas-fir beetle frass, (4) presence or absence of pitch streaming; and (5) pitch-exudation class (high, many large and recent streams; medium, intermediate-sized recent streams; low, one small, recent stream; or none). In addition, for up to three dominant live and three dominant recently-killed Douglas-fir (mortality status 0 or 1) per subplot, I also recorded presence or absence of root-rot mycelia (*Armillaria* spp.) beneath the bark at soil-level. This was accomplished by removing a 25 cm² section of bark and inspecting it for fungal mycelia. For each of these trees, I also quantified the relative amount of Douglas-fir beetle frass as the number of frass piles (high, five or more; medium, three to five; low = one to two; or none). In 2017, I sampled the same plots but used a more targeted approach by measuring variables specific to Douglas-fir (canopy thinning, mortality status, frass presence), and noted changes in vigor and biotic mortality agents relative to 2016. One site was not sampled in 2017 due to a lack of Douglas-fir. Douglas-fir that had root-rot mycelia in 2016 were not re-checked for mycelia in 2017.

Analyses

Prior to analyses, I re-assigned each site to a mortality class based on my empirical data. Using live and dead Douglas-fir from 2016, I computed a percent mortality for each site. Sites with <15% mortality were classified as having ‘low mortality’, those with 15 to 30% mortality as ‘medium mortality’, and those with $\geq 30\%$ mortality as ‘high mortality’ (Fig. 3.4).

For each study site and sampling year (2016 and 2017), I computed the proportion of Douglas-fir (1) exuding medium to high levels of pitch, (2) with any external beetle frass, (3) with

any root-rot mycelia, and (4) having both frass and root rot. I also estimated the proportion of living and dead Douglas-fir in both years, and the mean DBH of Douglas-fir. The amount of Douglas-fir thinning at each site was estimated by calculating the proportion of Douglas-fir stems with medium- to high-level canopy loss. Using measurements from all stems in each study sites, I also estimated the mean TPA, the proportion of stems that were Douglas-fir, the total study site basal area, and the proportion of basal area in Douglas-fir. Using data from the USGS DEM, I also estimated the elevation (MSL), aspect, and slope for each study site. To account for hilliness, I also considered the mean standard deviation of slope across subplots and the coefficient of variation of slope.

Using data from 2016, I examined associations of the above variables with the proportion of Douglas-fir mortality in 2017, as well as with the proportion of Douglas-fir with beetle frass, root rot mycelia, and both frass and root rot in 2017. A logit transformation ($\log_e(\text{proportion}/(1 - \text{proportion}))$) was applied to each response variable to stabilize variance, and zero values were increased by 0.001 to permit the \log_e transformation. To explore these relationships, I used a method similar to stepwise regression: least absolute shrinkage and selection operator (LASSO; Tibshirani 1996), using the glmnet package (Friedman et al. 2010) in R (R Core Team 2000). An example of this approach is presented in Figure 3.5. I performed ten LASSO regressions and chose the mean coefficient value for each predictor variable.

3.4 RESULTS

Among the 18 sites originally classified equally among mortality groups, six were found to be high mortality, eight medium mortality, and three low mortality. One site did not contain Douglas-fir, so it was not included in analyses. Each of the three new mortality classes was

significantly different from the other two in 2016 ($P < 0.01$). High mortality sites had a mean of 38.8% ($\pm 6.2\%$) standing dead Douglas-fir, medium mortality sites had a mean of 19.5% ($\pm 4.4\%$), and low mortality sites had a mean of 12.9% ($\pm 1.8\%$) (Fig. 3.4, Table 3.2).

Mortality rates of Douglas-fir tended to decline with elevation (Fig. 3.6) and slope (Fig. 3.7). Sites with lower mortality spanned a greater range of elevations and slopes. Mortality rates also tended to decline with mean diameter (DBH) within a site (Fig. 3.8). Sites with lower mortality spanned a greater range of mean diameters. However, sites that had greater proportional basal area of Douglas-fir, tended to be high-mortality sites (Fig. 3.9, Table 3.1).

The relationship between mortality and percentage of trees with medium to high pitch-exudation did not vary among high and medium mortality sites in either year (Fig. 3.10). Most of the low-mortality sites had similar percentages of trees with medium to high pitch-exudation (Fig. 3.10), suggesting that Douglas-fir beetle attacks have occurred at all sampled sites at the CRMW. In contrast, successful beetle attacks, as characterized by the presence of frass, were most associated with high and medium-mortality sites; frass was rarely present in low-mortality sites (Fig. 3.11). Root-rot mycelia were found at all high-mortality sites, some medium-mortality sites, but never in low-mortality sites (Fig. 3.12). When considering the joint occurrence of frass and root-rot mycelia, 66.7% of high mortality and 62.5% of medium mortality sites had both biotic agents (Fig. 3.13, Table 3.2).

The LASSO regression analysis indicated the combination of significant predictors (2016) for each response (2017) (Table 3.3). Site-level Douglas-fir mortality was negatively related to mean Douglas-fir DBH, positively related to proportion of Douglas-fir stems, the proportion of dominant living to dead Douglas-fir from a selected subset, and the standard deviation of slope. Additionally, a t-test revealed that the relationship between site mortality and aspect is positive for

south-facing stands. Root rot and frass were both related to the same set of predictor variables: frass presence in the previous year (2016), proportion of Douglas-fir stems, and standard deviation of slope (Table 3.3). Root rot and frass presence as a single response variables were only related to combined presence of root rot and frass in the previous year (2016) and elevation. After the removal of combined 2016 root rot and frass presence as a predictor variable because of suspected collinearity, the combined 2016 and 2017 root rot and frass presence model was found to be affected by proportion of selected dominant living to dead Douglas-fir living and elevation.

3.5 DISCUSSION

The positive associations between proportion of stems represented by Douglas-fir and bark-beetle infestation presence, and stand-level presence of *Armillaria* spp. root rot mycelium (Table 3.3), indicates a relationship between stand density, diversity, and plant pathogen dynamics. Douglas-fir mortality rates were higher in high-density stands of conspecifics, which could result from the stress that occurs as a result of the self-thinning process during canopy closure (He and Duncan 2000, Baleshta et al. 2005). Younger stands (<80 yrs. old) tend to be dominated by Douglas-fir, where shading stresses less dominant trees (Getzin et al. 2006). *Armillaria* spp. can take advantage of their closely adjacent roots (Van Der Kamp 1995), and this additional physiological stress could reduce the production of secondary metabolites important in repelling bark beetle attacks (Nebeker et al. 1995). Additionally, the negative association between standard deviation of stand slope and root rot infection suggests that smaller-scale topographic variability affects the ability of *Armillaria* spp. to spread within a stand (Cruickshank et al. 1997, Powers et al. 1999).

The presence of beetle frass was associated with similar factors as presence of root rot (Table 3.3). Presence of frass in 2017 was significantly predicted by the presence of frass from the previous year. Although frass was less common in 2017, stands with beetle infestations in 2016 continued to be attacked in the following year (Fig. 3.11). This pattern is indicative of Douglas-fir beetle infestations, which are generally spatially aggregated, often because live tree attacking bark beetles tend to be associated with spatially-contiguous disturbances (Powers et al. 1999). The positive association between the proportion of stems represented by Douglas-fir and bark beetle attacks likely reflects stand-scale Douglas-fir bark beetle infestations requiring high host tree density relative to other species. Although low host tree density stands can support endemic bark beetle populations, more abundant hosts are needed to support higher-density populations (Dodds 2003). The negative association between slope standard deviation and bark beetle attacks could reflect differences in water availability in sites with greater variation in slope in which drought stress limits the host tree defensive response to bark beetle attack (Van Mantgem et al. 2009).

Stands experiencing simultaneous root rot infection and bark beetle attack were associated with a different set of predictors than those experiencing these disturbance agents independently (Table 3.3). Higher stand proportions of living dominant Douglas-fir were negatively associated with root rot and bark beetle co-occurrence when removing root rot and frass presence from the previous year as a predictor. It is plausible that healthy Douglas-fir stems are an indication of stand resilience to attack from biotic agents (Bible 2001, Negrón et al. 2001). Elevation was also negatively associated with concurrent root rot presence and bark beetle attack, which has been previously reported for other bark beetle systems (Powers et al. 1999, Bentz et al. 2010). However, at CRMW, the relationship to elevation might reflect greater past logging at lower elevations, resulting in higher-elevation sites being considerably older and more diverse, and consequently

less conducive to the spread of *Armillaria* spp. and high-density Douglas-fir beetle populations (Dodds 2003, Baleshta et al. 2005, Cruickshank et al. 2009).

Past work has shown that mature stands with larger trees generally have lower annual mortality rates (Bible 2001). These stands tend to have overall lower stem density, and as a result, lower root density, lower root competition, and a reduced vulnerability to root rot diseases (Peet et al. 1996). Mature stands also tend to have more established, vigorous trees with reduced intra- and interspecific competition. Consequently, these stands are less susceptible to biotic infestation, and generally succumb to infestations as individual trees as a result of age-dependent factors rather than outbreaks by biotic agents (Li 2014). Mortality at the CRMW followed this pattern, as stands with larger Douglas-fir had significantly less mortality (Table 3.3).

The LASSO regression technique was helpful in identifying a set of significant predictors from a larger set of potential predictors. The technique is thought to have advantages over traditional stepwise regression methods in terms of model selection and parameterization (Osborne et al. 2000, Zou 2006). However, there were trends in the pattern of mortality even when the LASSO technique did not statistically identify these trends. For example, the presence of Douglas-fir beetle frass had a strong relationship with mortality (Fig. 3.11), even though frass was not identified as a significant predictor of mortality (Table 3.3). Low mortality stands had very little or no sign of Douglas-fir beetle attack, while most medium and nearly all high mortality sites had signs of beetle attack (Fig. 3.11). Douglas-fir beetle often fails to successfully colonize non-immunosuppressed trees, and stands without other physiological stressors or adjacent infestations rarely support successful beetle attacks (Furniss et al. 1979, Lessard and Schmid 1990). Since Douglas-fir beetles only attack living trees, medium mortality stands at the CRMW might have been experiencing new or growing infestations (Wood 1982, Ross and Daterman 1995). In high

mortality stands, the remaining host trees might have been insufficient to sustain additional beetle infestations.

The lack of a relationship between mortality and co-occurrence of root rot and beetle frass runs counter to past observations of stand fungal-pathogen dynamics (Nebeker et al. 1995, Van Der Kamp 1995, Rosso and Hansen 1998). However, because Douglas-fir beetles require living Douglas-fir as hosts, high-mortality stands may not have the capacity to support new beetle attacks as do medium-mortality stands. Additionally, root rot and bark beetles do not always kill their host trees within 1-2 years; rather, this process can take up to a decade or more (Morrison and Mallett 1996). At the CRMW, there did not appear to be a relationship between the co-occurrence of root rot and bark beetle frass, and stand mortality (Fig. 3.13).

In the CRMW, most Douglas-fir stands are ~80-100 years old, especially in the lower elevations where the high-mortality sites tended to be located. At this age, individual tree mortality generally does not occur until 10-20 years after the initial root rot infection (Bloomberg and Morrison 1989, Morrison and Mallett 1996, Cruickshank et al. 2009). Thus, the spatially widespread trend in mortality at the CRMW suggests there are factors that are driving these patterns which may not be strongly identifiable over a two-year study period. The unusually high mortality levels observed in certain stands within the CRMW could be a combined result of topographic stand conditions and recent climate trends that increase Douglas-fir physiological stress, which in turn could predispose Douglas-fir to pathogens, Douglas-fir beetle, and other biotic agents that host trees might otherwise be able to overcome through plant defenses. Indeed, landscape-scale disturbances are known to be associated with higher temperatures and drought, which could be exacerbated by stand successional conditions (Christiansen et al. 1987, Powers et al. 1999, He and Duncan 2000). Mortality events directly or indirectly driven by climate have

become more common in the last 20 years throughout the Pacific Northwest (Cohen et al. 2016). A longer-term study of the mortality dynamics in the CRMW could elucidate similar relationships. In this study, I provided baseline conditions and an assessment of the potential drivers of mortality trends in the CRMW, which should motivate future questions regarding forest health in this watershed.

3.6 REFERENCES

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TABLES

Table 2.1. Degree day values at varying percentiles of early season Douglas-fir beetle flight, and the mean calendar day at which these degree days are obtained using temperature data measured at the CRMW over the sampled years (2005, 2007-2010, 2015-2017). and the estimated degree days. Also shown is the expected calendar day at which the listed degree days are obtained when assuming the B1 climate change scenario (+ 1.7 °C) at out study sites.

Percent of Flight	Degree Days	Calendar Day Observed	Calendar Day +1.7 °C
5%	86.7	87	60
10%	134.0	102	80
25%	223.5	125	104
50%	344.5	148	125
75%	501.4	168	146
90%	677.3	187	164
95%	801.6	197	175

Table 3.1. Physical plot metrics acquired via in-situ measurement in 2016 (trees per acre [TPA], total basal area [BA], and Douglas-fir BA), historical records (stand age), or DEM models (latitude/longitude, slope, aspect, and elevation).

PSP ID	Latitude, Longitude	Slope \pm SD (degrees)	Aspect	Elevation (m)	Stand Age (Year)	TPA	Total BA (cm)	Douglas-fir BA (cm)
2207242128	47.38686, -121.86231	8.14 \pm 6.51	S	226.54	1906-1945	169.03	756.18	589.02
2	47.38584, -121.90918	1.52 \pm 1.29	S	215.66	1906-1945	358.15	612.26	507.14
2208074128	47.40677, -121.83390	4.62 \pm 0.66	S	291.52	1906-1945	422.90	828.61	727.91
2308322128	47.43658, -121.81255	17.72 \pm 3.37	S	777.71	1906-1945	284.23	813.35	442.88
2207221128	47.38638, -121.89194	3.7 \pm 2.46	N	209.80	1906-1945	182.14	590.54	512.43
4	47.37684, -121.90877	5.6 \pm 11.37	E	215.57	1906-1945	237.84	356.25	331.84
2207091128	47.41587, -121.91409	6.53 \pm 2.68	W	281.50	1906-1945	202.92	897.30	795.24
2109114128	47.31956, -121.62181	15.52 \pm 3.15	N	717.27	1906-1945	969.62	746.97	210.25
2207181128	47.39558, -121.95720	13.68 \pm 12.22	S	213.96	1906-1945	212.50	320.80	180.93
19	47.39185, -121.82462	4.54 \pm 1.38	W	415.82	1906-1945	255.38	606.75	544.65
2208343128	47.34799, -121.77462	19.22 \pm 5.79	W	554.86	1906-1945	272.50	608.92	275.10
2208014128	47.41756, -121.72492	2.34 \pm 0.3	S	475.60	1906-1945	241.15	759.69	341.85
2207162128	47.39602, -121.92827	3.42 \pm 2.03	E	231.08	1906-1945	172.31	691.79	534.88
13	47.39133, -121.84808	10.54 \pm 9.78	N	227.30	1906-1945	198.53	836.78	710.81
2110033128	47.33004, -121.52760	20.56 \pm 11.73	W	721.24	1946-1975	795.63	470.15	135.75
20	47.36166, -121.81029	2.26 \pm 0.9	S	399.36	1906-1945	183.48	1045.52	715.00
2110163128	47.30043, -121.54926	28.64 \pm 6.86	E	1040.58	>1855	170.00	770.25	197.94

Table 3.2. Proportion of standing dead Douglas-fir stems to all Douglas-fir stems and associated general mortality classification (high: > 0.30 standing dead to all stems; medium: 0.15 to 0.30; and low: < 0.15), and proportion of Douglas-fir stems affected by biotic mortality agents to all Douglas-fir stems.

PSP ID	Mortality Class	Proportion Douglas-Fir Standing Dead		Proportion Douglas-Fir with Frass		Proportion Dead Douglas-Fir with Root Rot		Proportion Douglas-Fir with Root Rot & Frass	
		2016	2017	2016	2017	2016	2017	2016	2017
2207242128	High	0.446	0.561	0.387	0.192	0.727	0.857	0.226	0.258
2	High	0.445	0.457	0.222	0.050	1.000	1.000	0.000	0.074
2208074128	High	0.442	0.497	0.161	0.097	0.438	0.625	0.097	0.097
2308322128	High	0.347	0.356	0.077	0.000	1.000	1.000	0.000	0.000
2207221128	High	0.336	0.342	0.036	0.110	0.500	0.500	0.000	0.000
4	High	0.313	0.314	0.135	0.029	0.875	0.909	0.135	0.135
2207091128	Medium	0.270	0.292	0.292	0.088	1.000	1.000	0.083	0.083
2109114128	Medium	0.252	0.281	0.000	0.000	0.000	0.000	0.000	0.000
2207181128	Medium	0.194	0.194	0.273	0.091	0.000	0.000	0.182	0.182
19	Medium	0.188	0.206	0.000	0.035	1.000	1.000	0.000	0.000
2208343128	Medium	0.188	0.188	0.000	0.000	0.000	0.000	0.000	0.000
2208014128	Medium	0.158	0.265	0.538	0.024	1.000	1.000	0.154	0.154
2207162128	Medium	0.156	0.187	0.346	0.067	1.000	1.000	0.154	0.154
13	Medium	0.152	0.152	0.206	0.121	0.667	0.778	0.118	0.147
2110033128	Low	0.147	0.191	0.000	0.011	0.000	0.000	0.000	0.000
20	Low	0.130	0.130	0.000	0.000	0.000	0.000	0.000	0.000
2110163128	Low	0.111	0.111	0.000	0.000	0.000	0.000	0.000	0.000

Table 4.3. Parameter coefficients of significant predictors measured in 2016 for Douglas-fir mortality, presence of root rot, frass, and root rot and frass measured in 2017. Dots denotes lack of significance; predictors excluded from the analysis are noted by “/” .

2016 Predictor	2017 Response Variable				
	Mortality	Root Rot	Frass	Root Rot & Frass	Root Rot & Frass ¹
Frass	.	5.9994	4.375	/	/
Root Rot	.	/	.	/	/
Root Rot & Frass	.	.	.	15.7830	/
Proportion Thinning	/
Pitch
Mean Douglas-fir DBH	-0.0081
Trees per Acre
Stand Proportion Douglas-fir	0.2073	8.4065	7.4374	.	.
Proportion Living Selected Stems	-2.3302	.	.	.	-0.5088
Douglas-fir Mortality	/
Stand Proportion Douglas-fir Basal Area
Total Stand Basal Area
Mean Slope
Slope Standard Deviation	-0.0012	-0.1045	-0.0385	.	.
Slope Coefficient of Variation
Aspect	. ²
Elevation	.	.	.	-0.0004	-0.0016

¹Root rot and frass predictors not included to eliminate redundancy.

²South-facing slopes were significantly correlated with increasing Douglas-fir mortality (P<0.01)

FIGURES

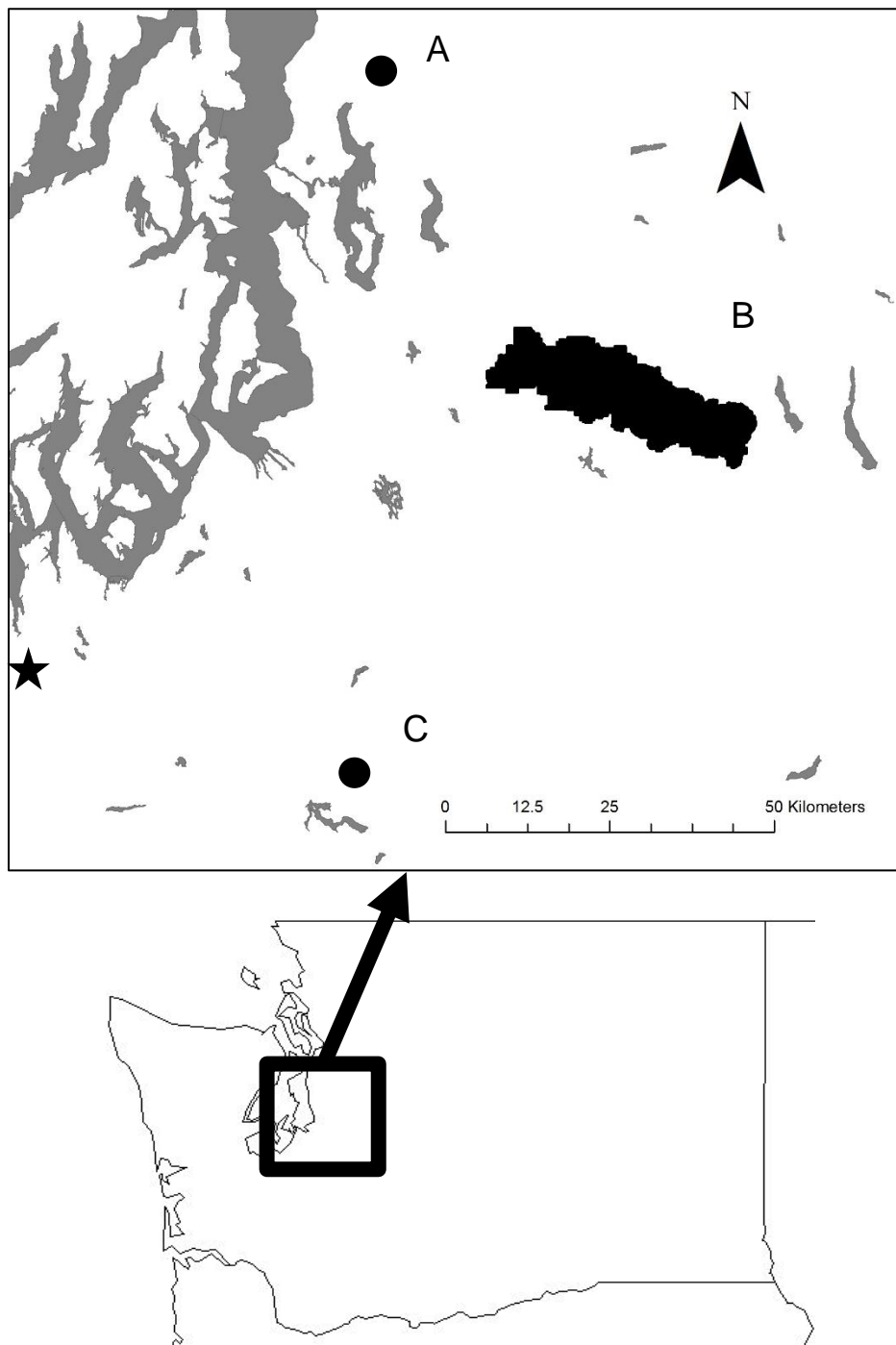


Figure 2.1. Locations of 2015-2017 field study locations: (A) Lee Memorial Forest (0.65 km²), (B) Cedar River Municipal Watershed (364 km²), and (C) Pack Experimental Forest (17.40 km²).



Figure 2.2. Lindgren 12-unit funnel trap used to sample Douglas-fir beetle. Lures include 6-ml low-release packet of ethanol (attached to top funnel), a packet containing 2745 μl of frontalin (1,5-dimethyl-6,8-dioxa-[3,2,1]-bicyclooctane) and 250 μl of seudenol (3-methyl-2-cyclohexen-1-ol) (attached to 6th funnel from bottom), and a 15 ml packet of Douglas-fir kairomone blend (2nd from bottom funnel). At the bottom of the funnels in a collection container (white) filled with propylene glycol, a nontoxic antifreeze.

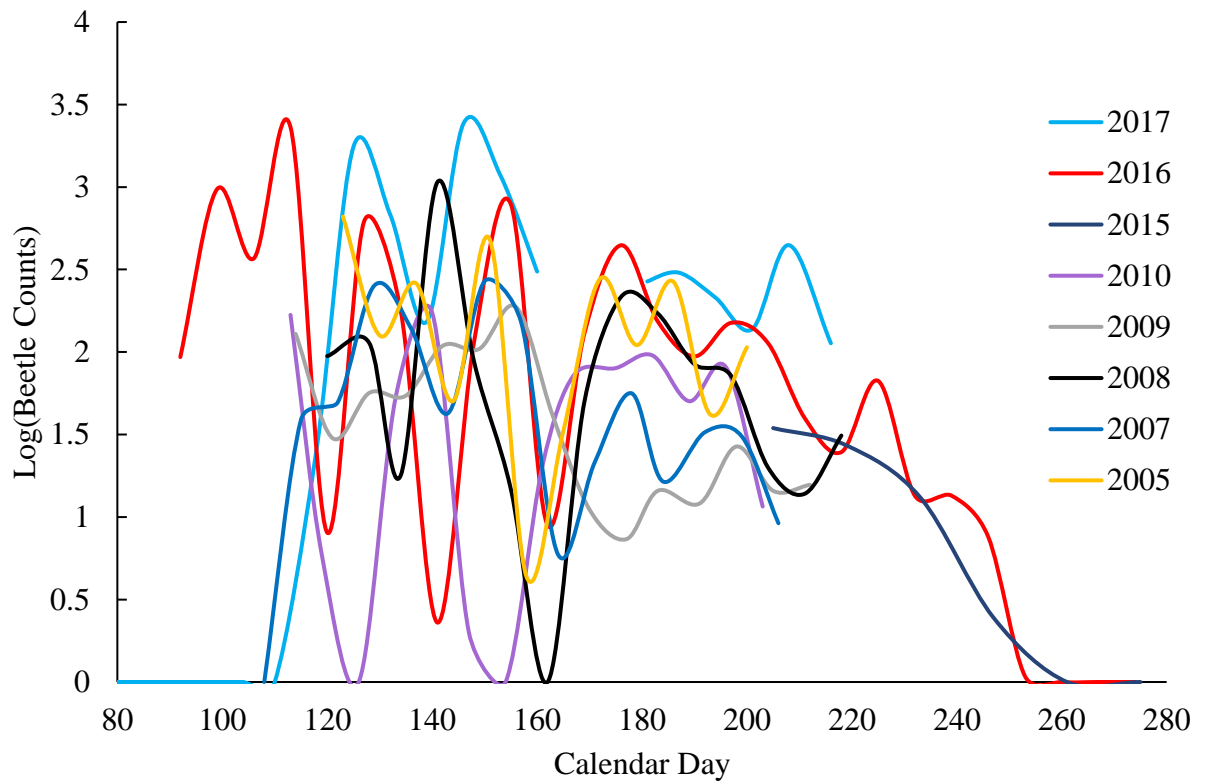


Figure 2.3. Trap catch data of Douglas-fir beetle (counts transformed using $\log_{10}(y+1)$) from Lindgren funnel traps (cf. Fig. 2.4) over calendar day at the Cedar River Municipal Watershed during sampled years.

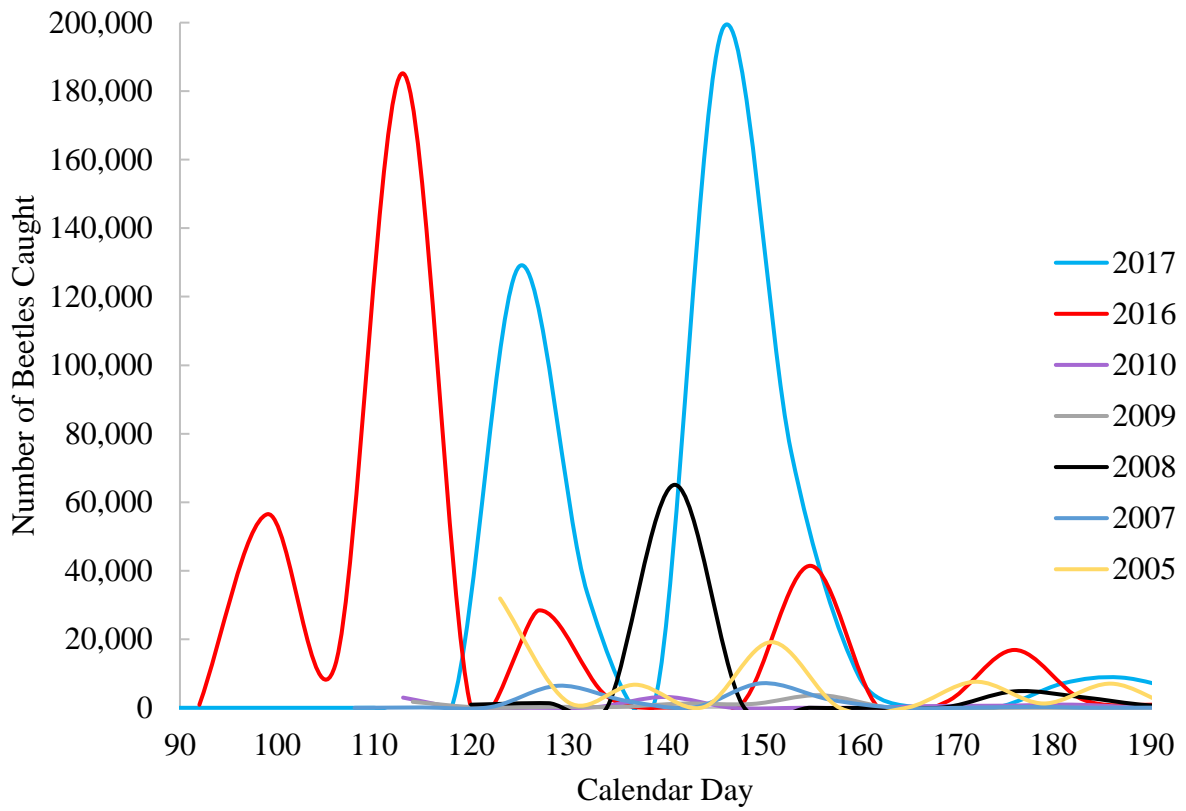


Figure 2.4. Mean weekly counts of Douglas-fir beetle from Lindgren funnel traps over the course of the sampling season at the Cedar River Municipal Watershed during sampled years.

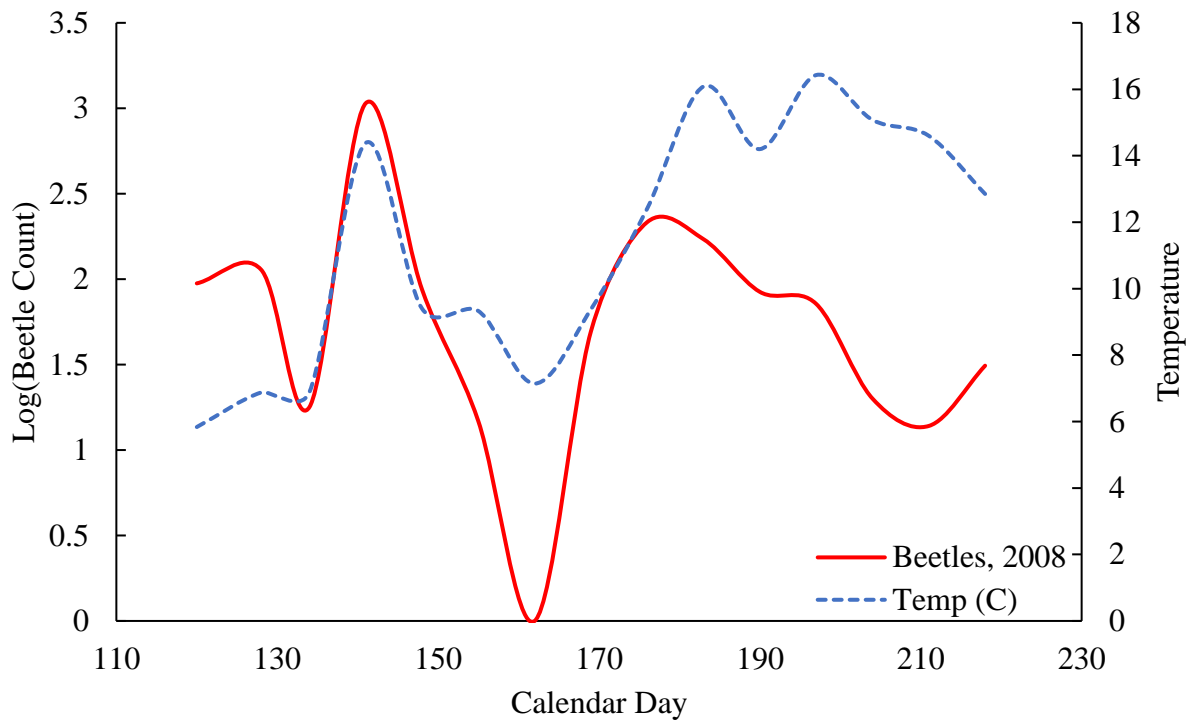


Figure 2.5. Log10 transformed beetle flight counts from the Cedar River Municipal Watershed (2008) with mean weekly temperature across collection season.

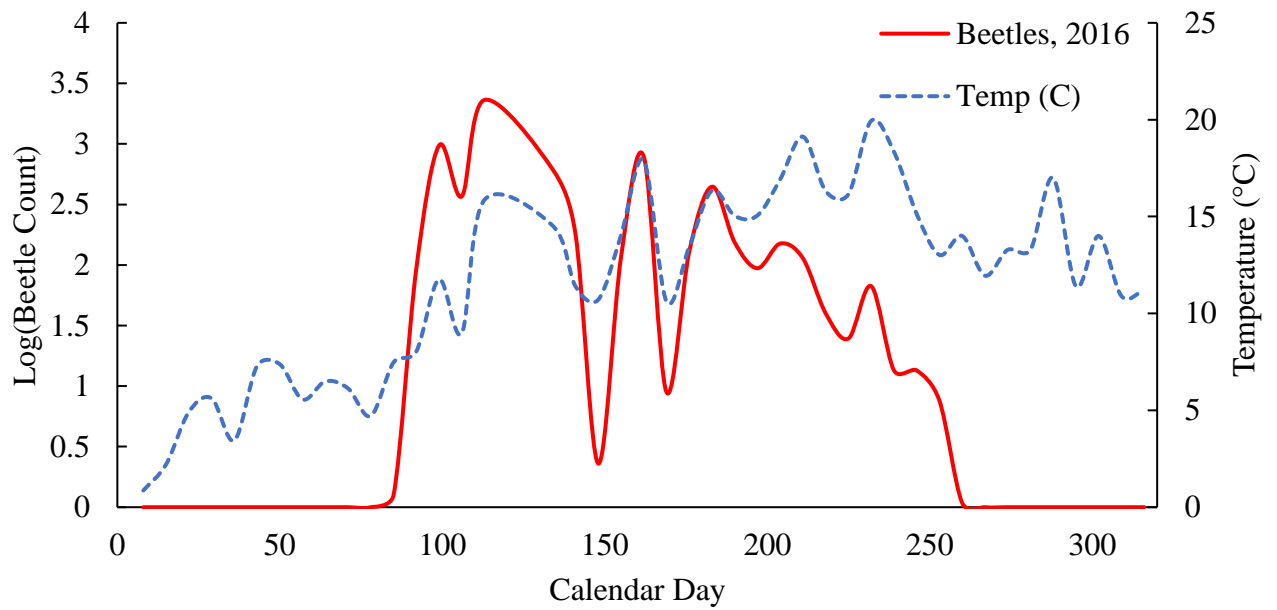


Figure 2.6. Log10 transformed beetle flight data from the Cedar River Municipal Watershed (2016) with mean weekly temperature across collection season.

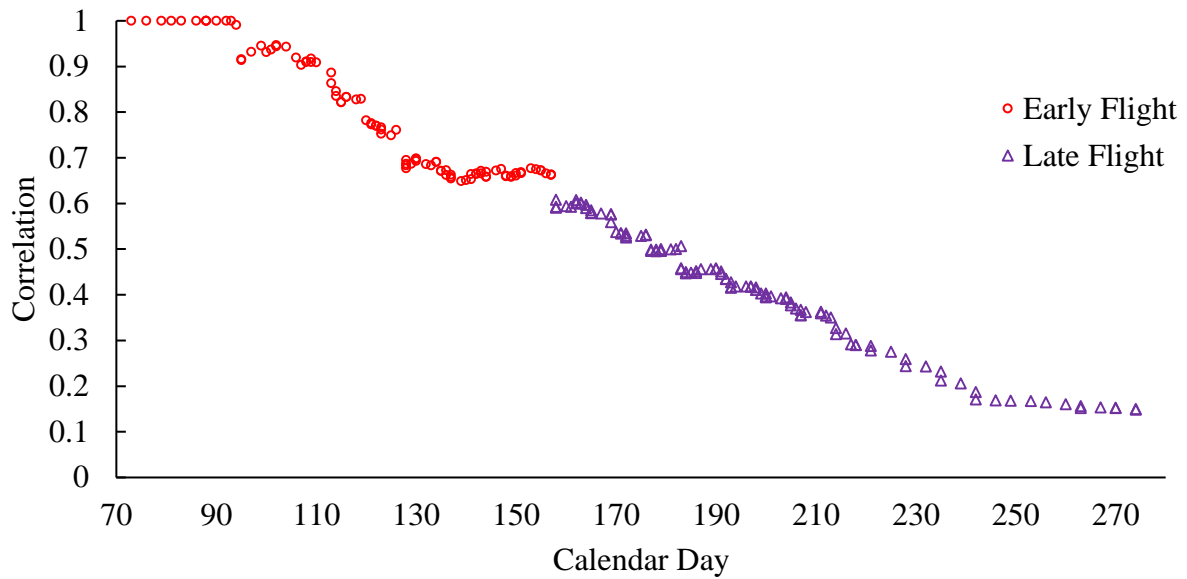


Figure 2.7. Estimates of Pearson's correlation coefficient between weekly log₁₀-transformed beetle counts and weekly mean temperature across all sites and years (2005, 2007-2010, 2015-2017). Significant correlation estimates are denoted by red circles and non-significant estimates are shown as purple triangles. Significance between these variables ended at day 157, from which I partitioned Douglas-fir beetle seasonality into early or late flight.

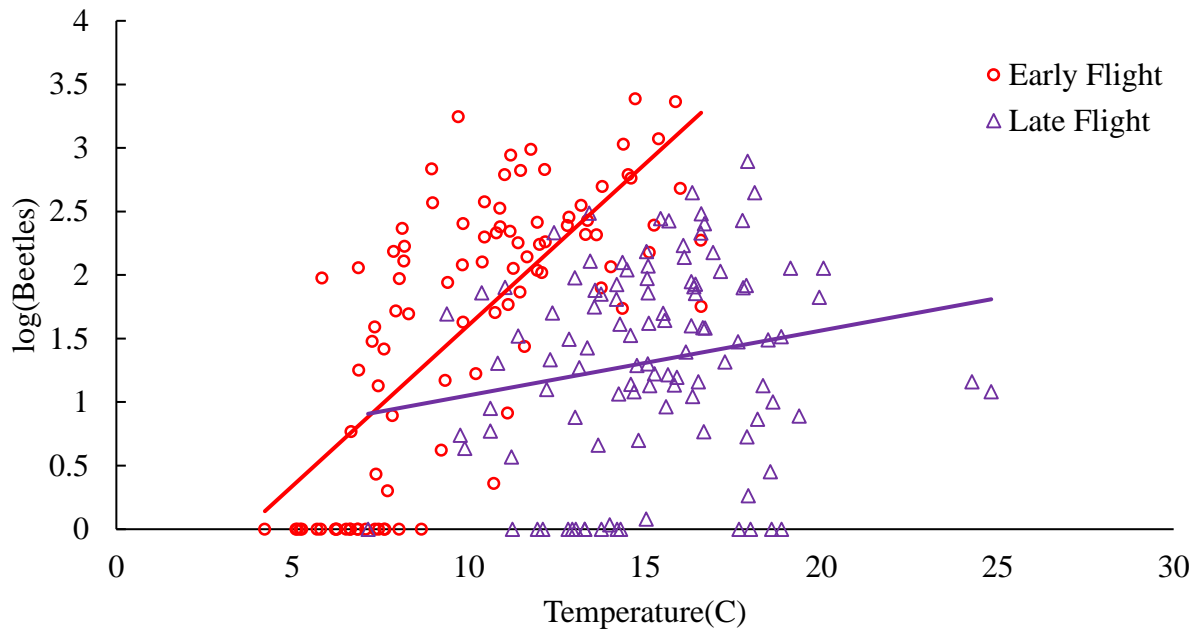


Figure 2.8. Correlative relationships between weekly \log_{10} -transformed beetle counts and weekly mean temperature across all sites and years (2005, 2007-2010, 2015-2017). Red circles represent early season beetle flight, a significant relationship with temperature ($\alpha=0.001$) while purple triangles represent late season flight, a non-significant relationship with temperature (cf Fig. 2.7).

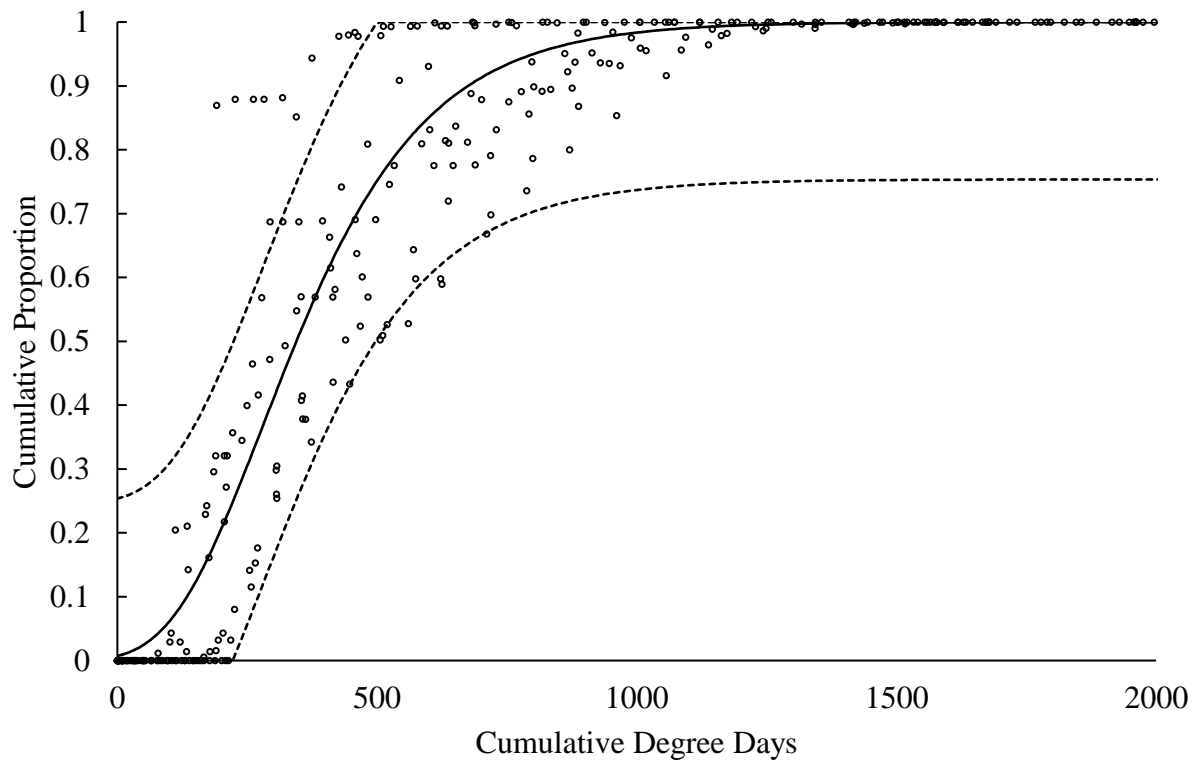


Figure 2.9. Cumulative proportion of beetles trapped in pheromone-baited traps, 2005, 2007-2010, 2016-2017, over accumulated degree-days above 4.3°C from January 1. Peak of beetle flight (cumulative proportion of 0.5) was reached at 344.5 degree-days. Values are overlaid by a nonlinear model curve with 5% and 95% confidence bands.

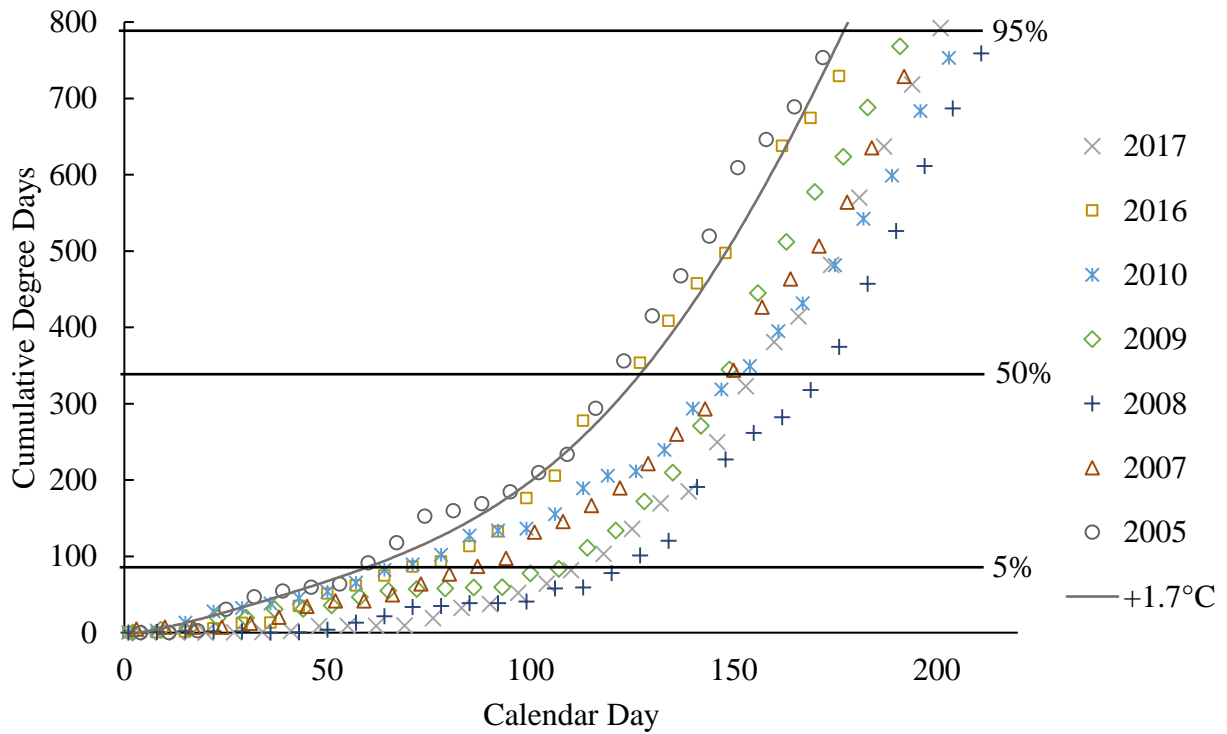


Figure 2.10. Cumulative degree days above 4.3°C at the Cedar River Municipal Watershed (2005, 2007-2010, 2016-2017), with IPCC projected 1.7°C mean increase (Intergovernmental Panel on Climate Change, 2014). Horizontal lines represent respective cumulative proportions of active beetle flight (see figure 2.1 and table 2.1).

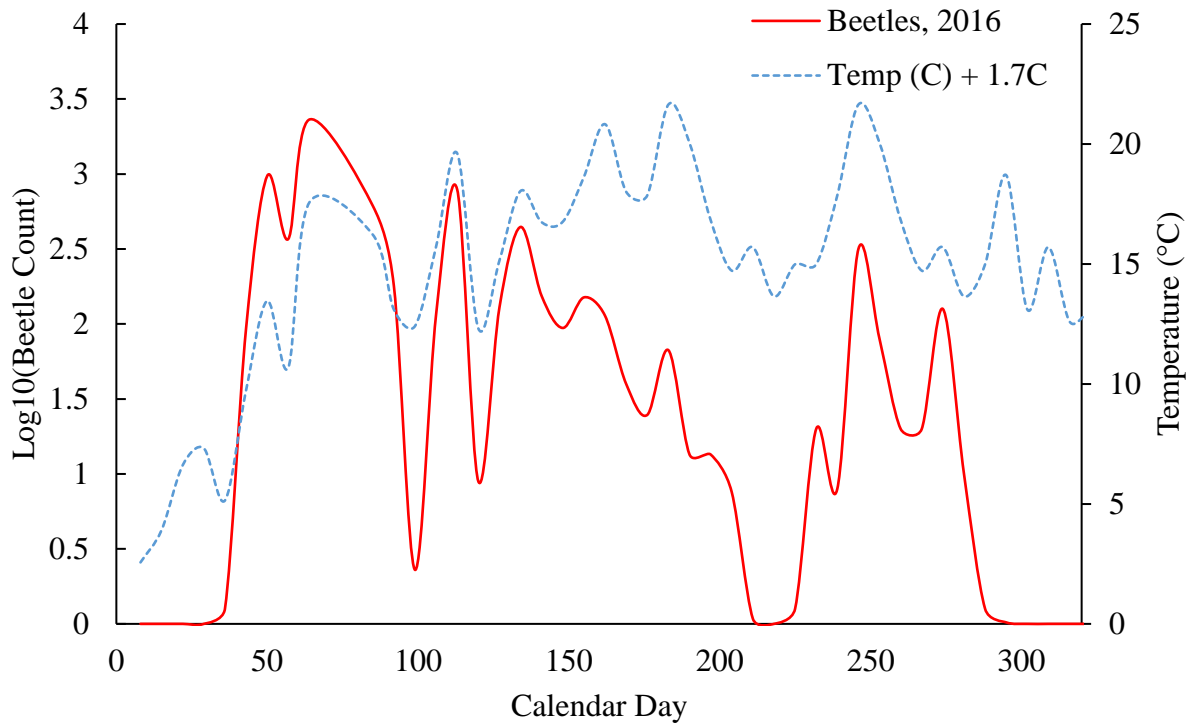


Figure 2.11. Log10 transformed beetle flight data from the Cedar River Municipal Watershed (2016) with mean weekly temperature increased by the IPCC B1 climate change scenario of 1.7°C across collection season (Intergovernmental Panel on Climate Change, 2014). Beetle flight and temperature data shifted earlier to demonstrate earlier emergence with higher spring temperatures and a second emergence cycle at the end of the lengthened active season.

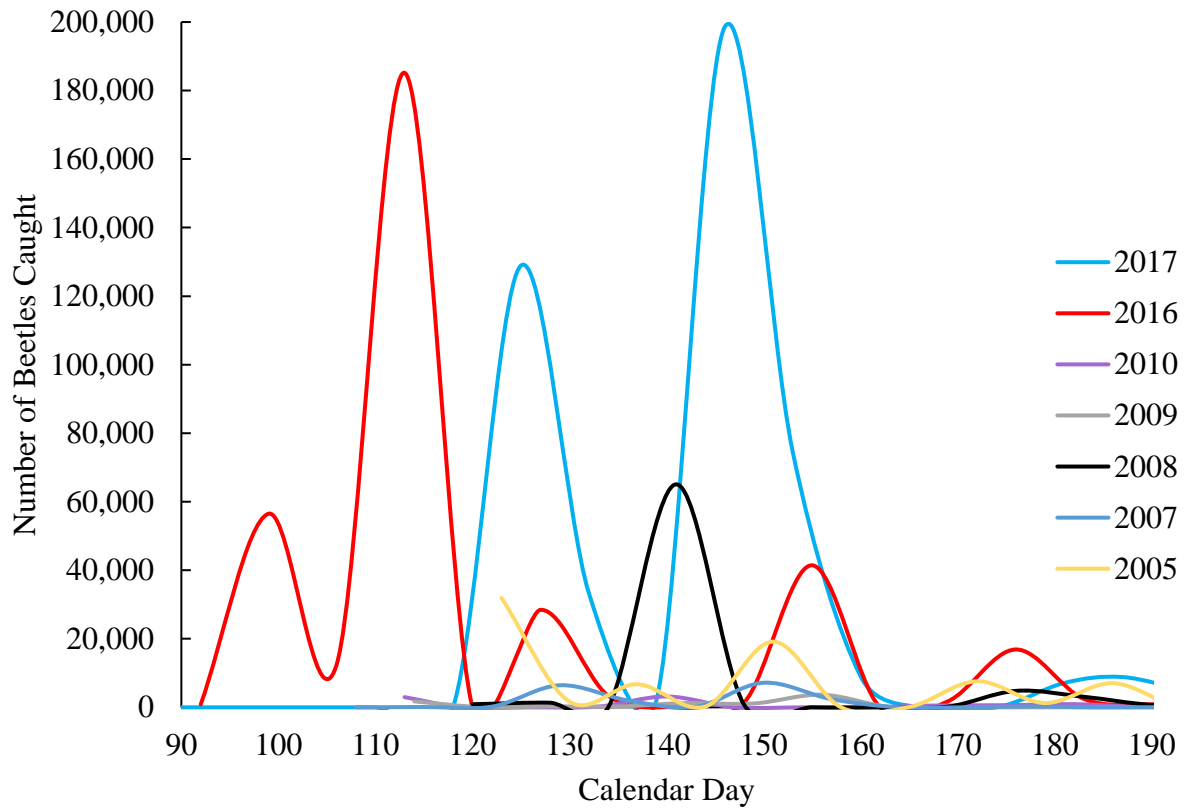


Figure 3.1. Mean trap catch of Douglas-fir beetle from Lindgren funnel traps over the course of the year at the Cedar River Municipal Watershed.

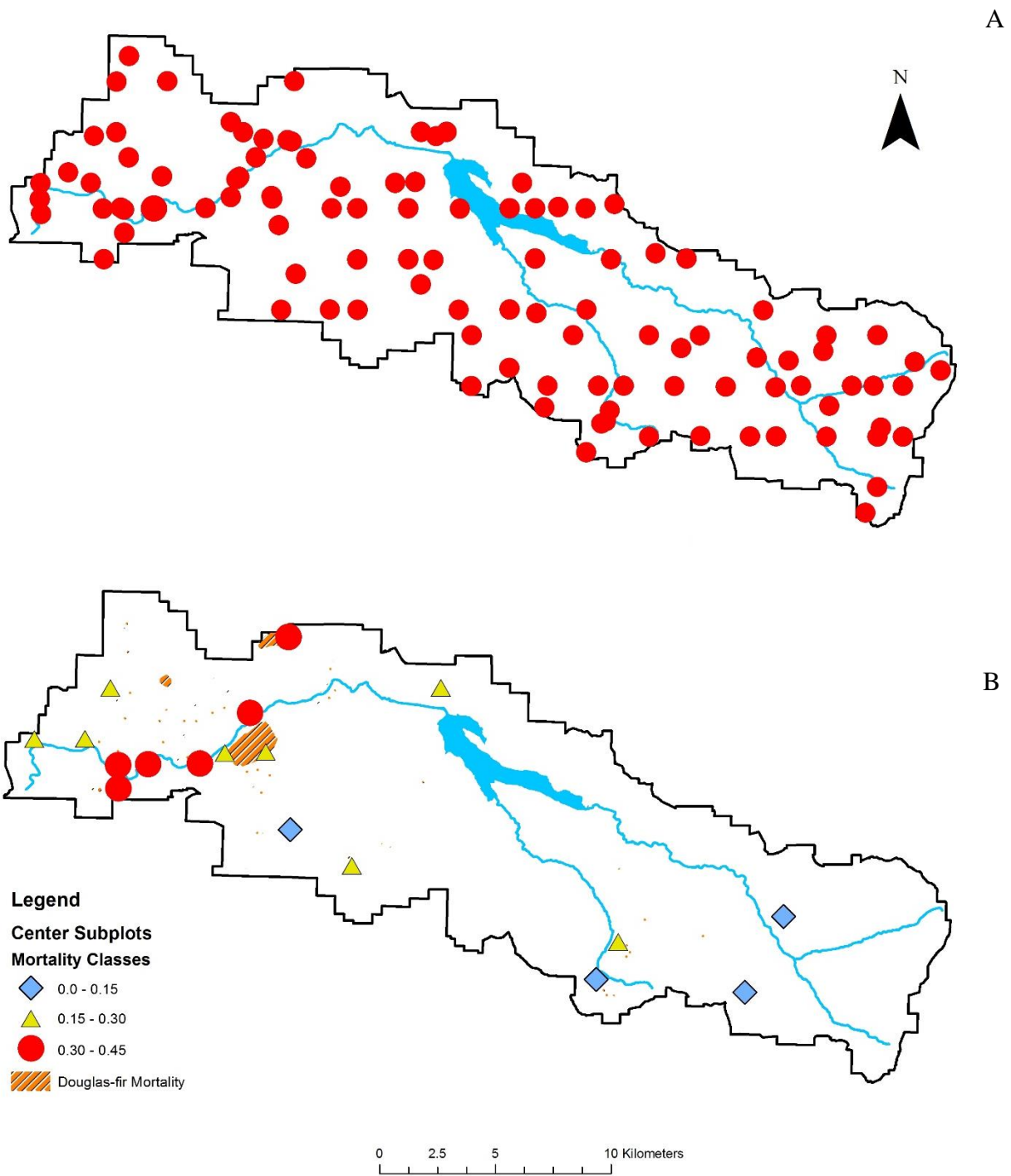


Figure 3.2. The Cedar River Municipal Watershed, WA, (A) with all historical permanent sampling plots (PSPs) and (B) with selected experimental sites by proportion of recorded mortality in 2016. Aerial survey data from 2015 indicate areas of Douglas-fir mortality.

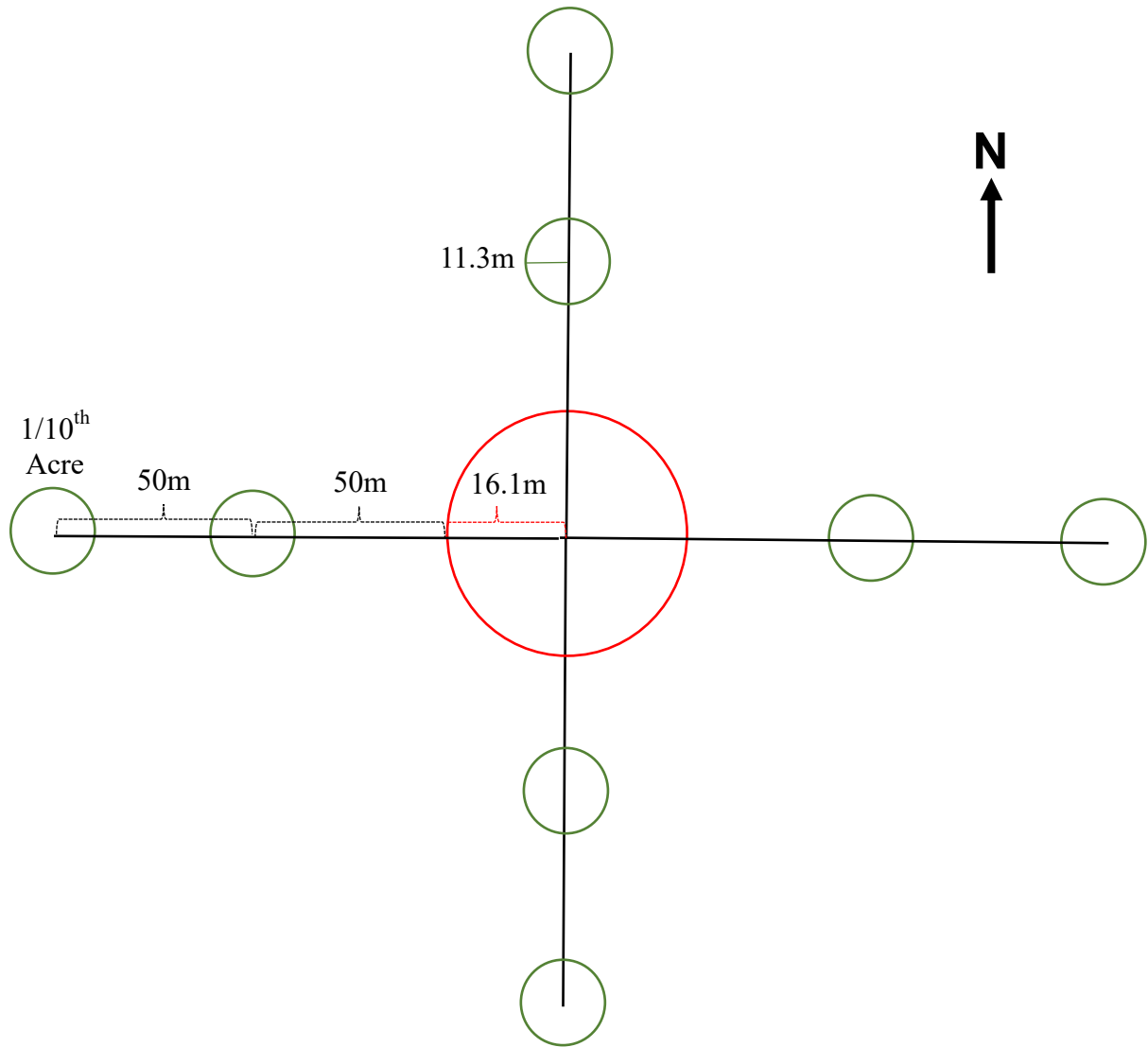


Figure 3.3. Spatial layout of 1/10th acre subplots around a selected 1/5th acre PSP plot.

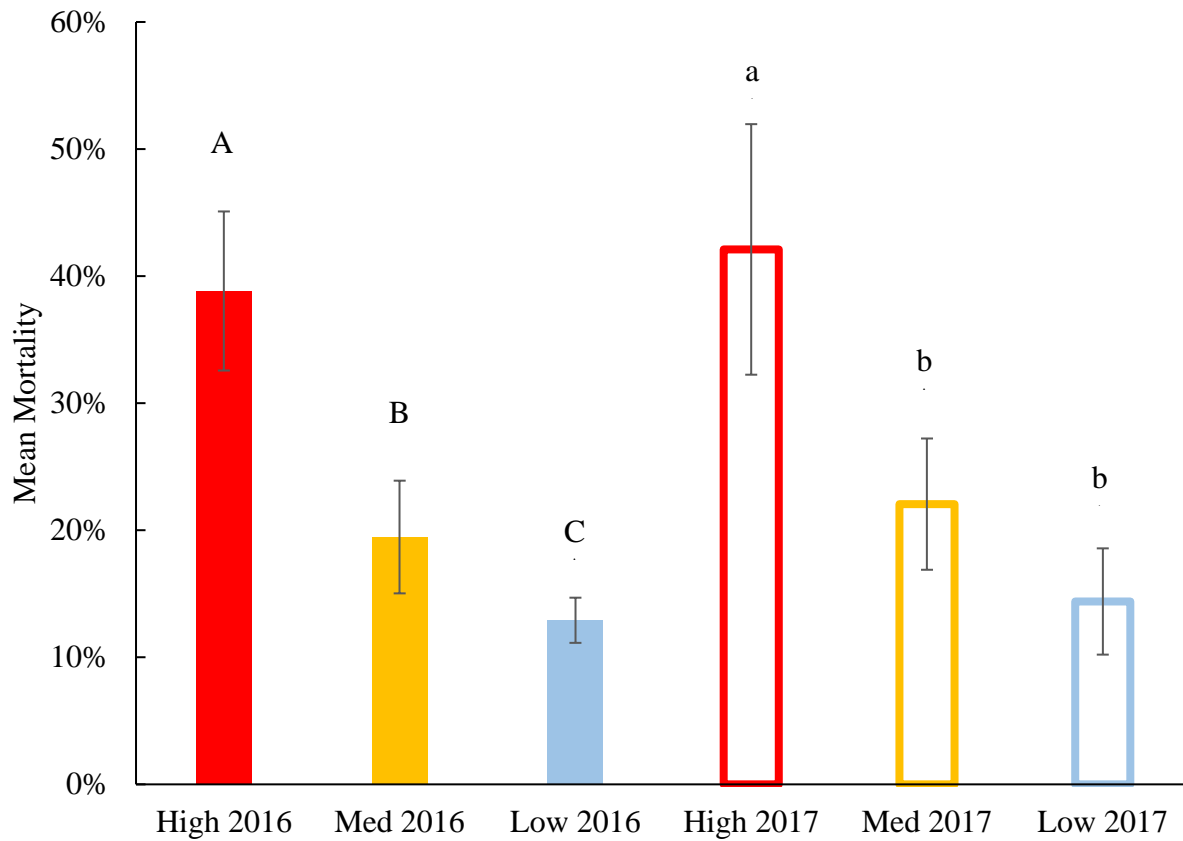


Figure 3.4. Mean percent of standing dead Douglas-fir (≥ 5 cm DBH) in 2016 and 2017. Mortality classifications (high, med, and low) in 2016 were based on data collected in 2016. All mortality levels in 2016 were significant different from each other ($P < 0.01$). High mortality in 2017 was significant different than medium and low classes ($P < 0.01$).

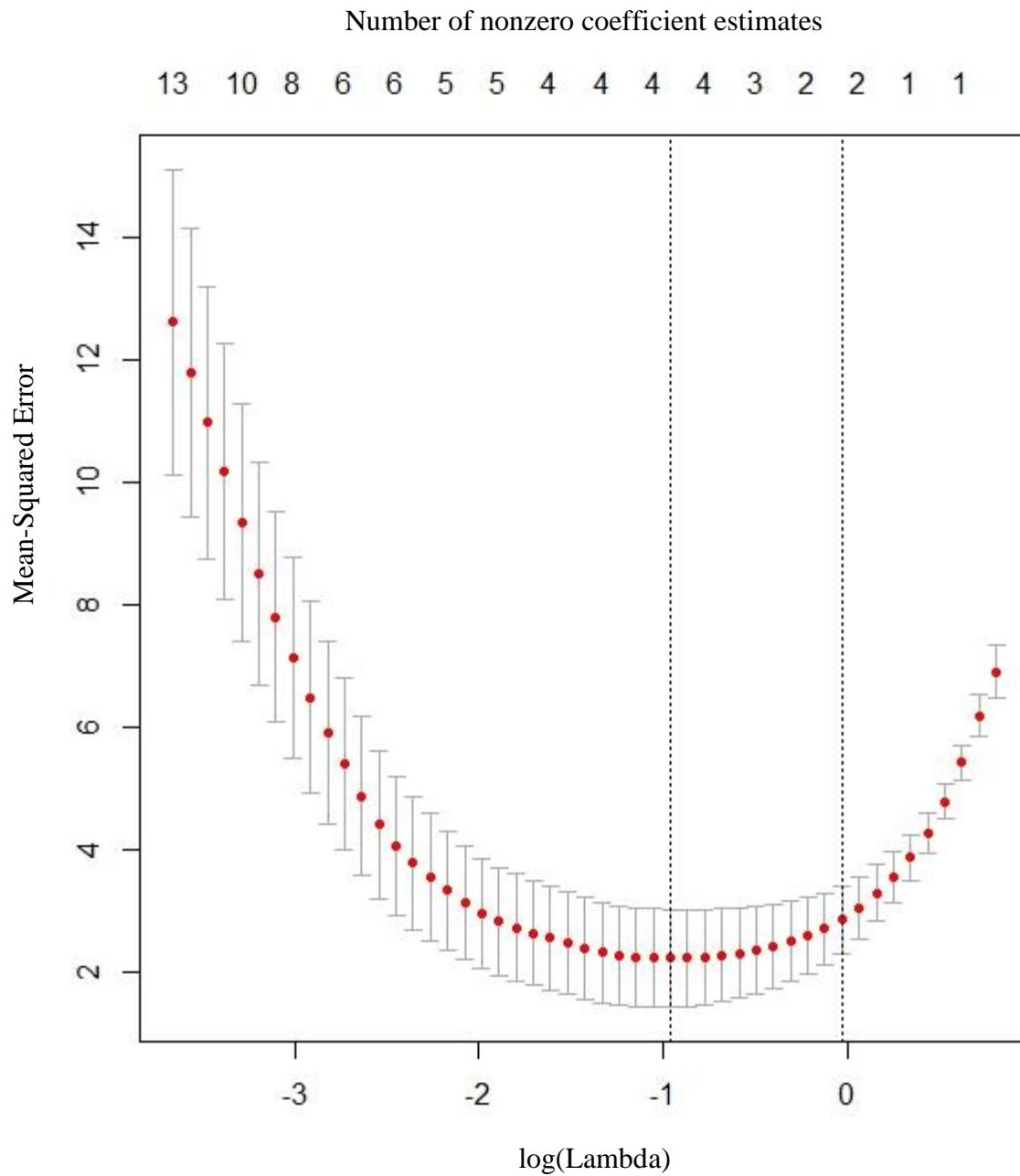


Figure 3.5. Example results from LASSO regression. Dotted vertical lines indicate λ_{\min} (right), which minimizes out-of-sample loss of the coefficient of variation, and λ_{1se} (left), the largest λ value within 1 standard error of λ_{\min} .

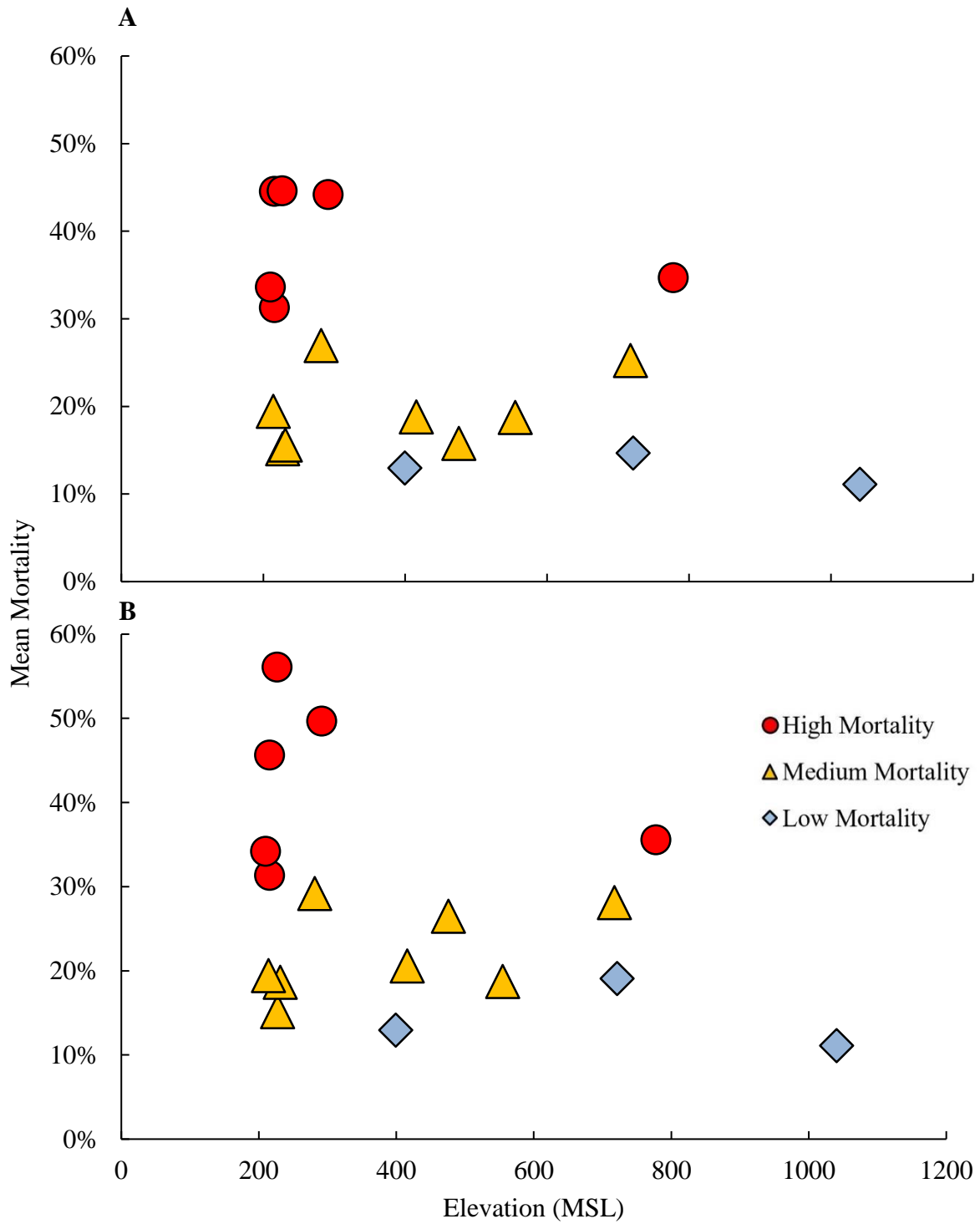


Figure 3.6. Mean percent of standing dead Douglas-fir for each mortality class by elevation (MSL) in 2016 (A) and 2017 (B).

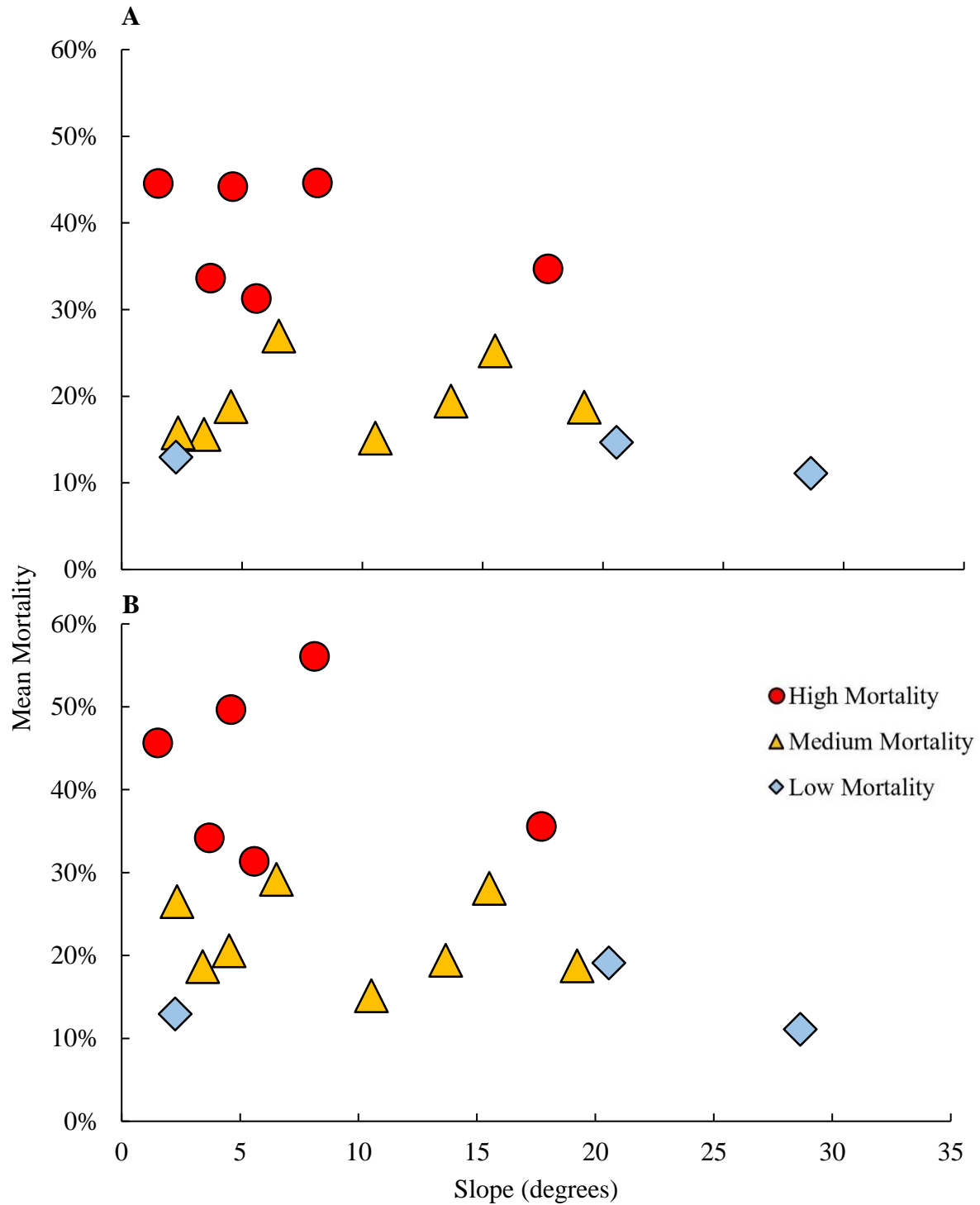


Figure 3.7. Mean percent of standing dead Douglas-fir for each mortality class by slope in 2016 (A) and 2017 (B).

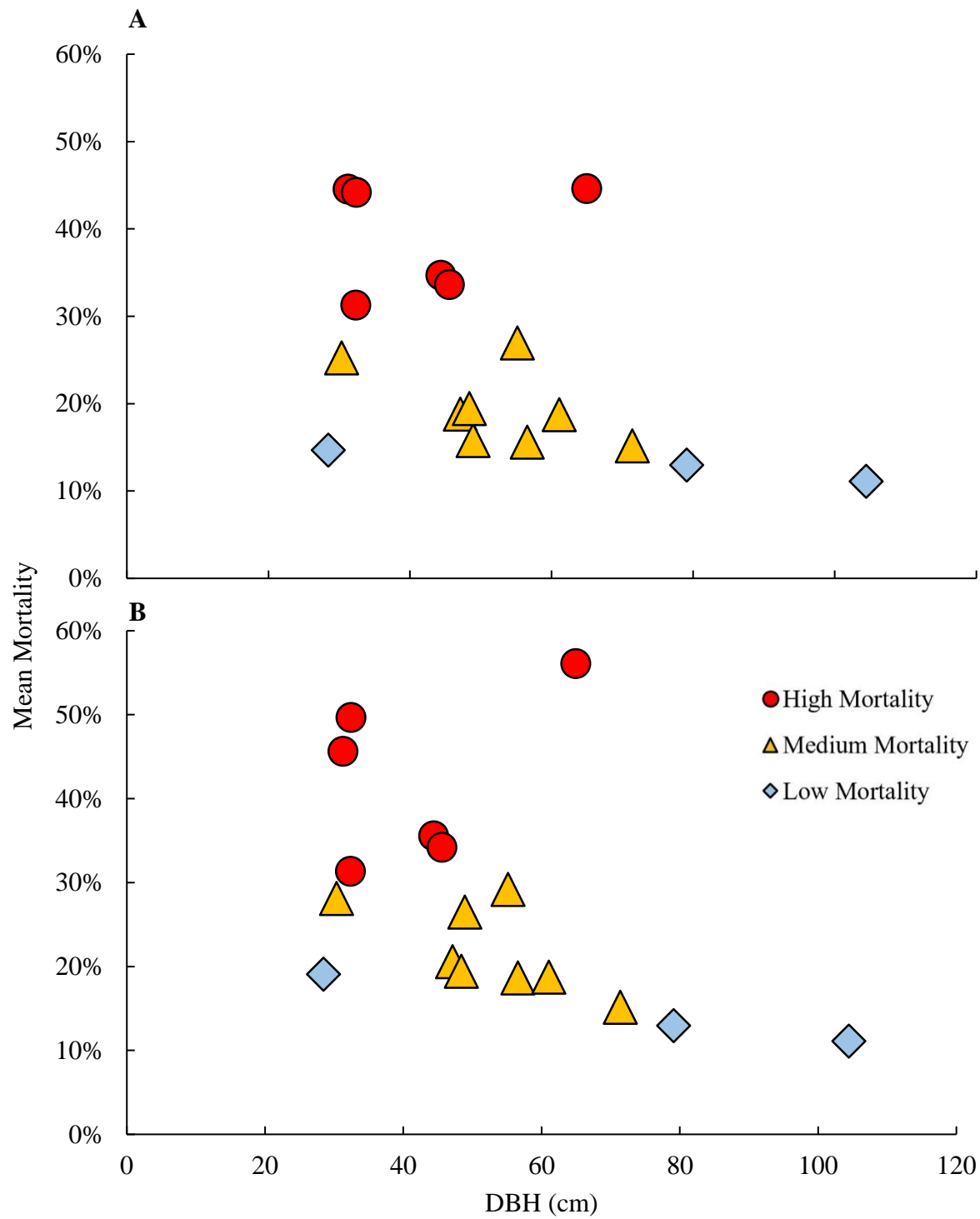


Figure 3.8. Mean percent of standing dead Douglas-fir for each mortality class by mean Douglas-fir diameter at breast height (DBH) in 2016 (A) and 2017 (B).

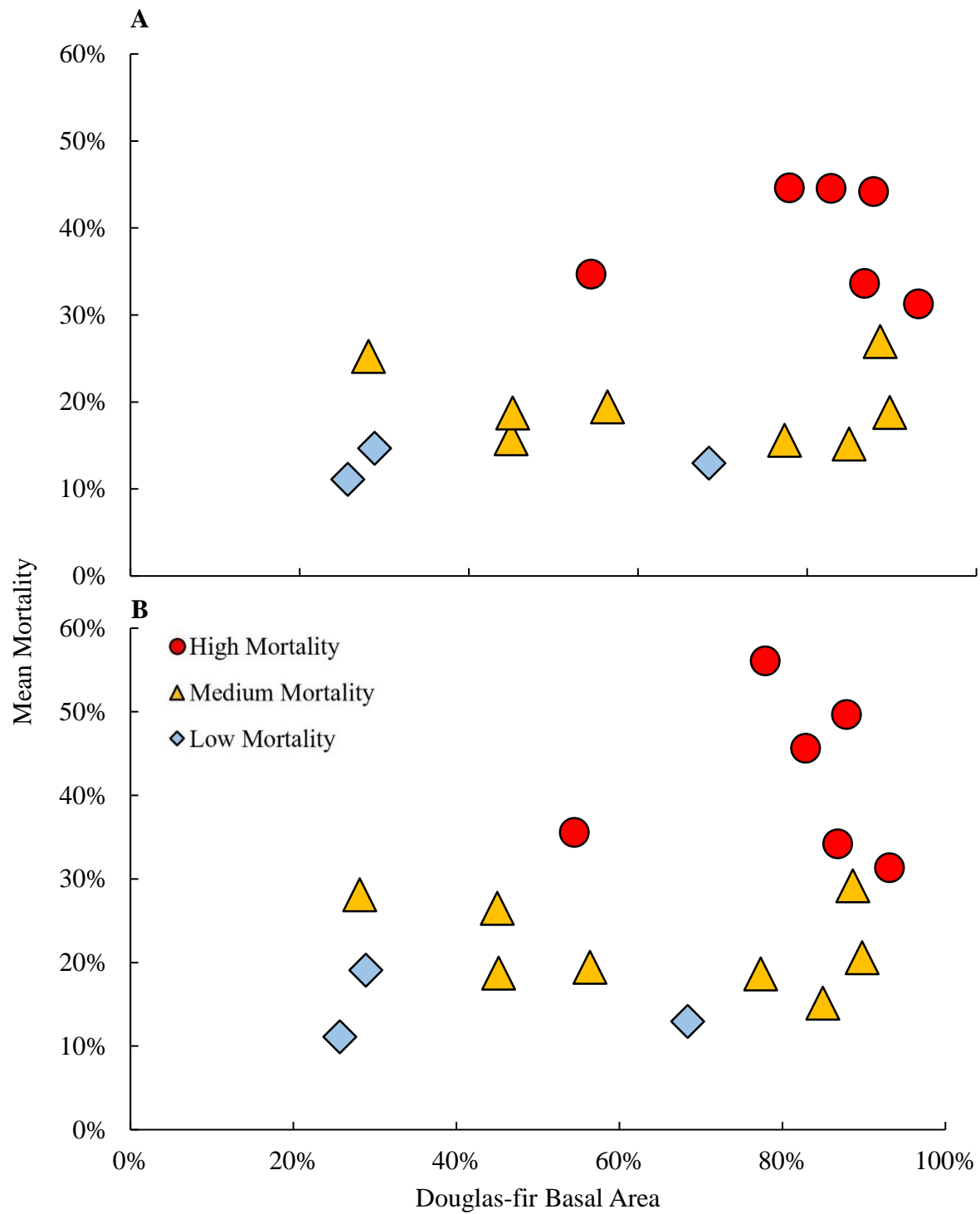


Figure 3.9. Mean percent of standing dead Douglas-fir for each mortality class by the percent of the site mean basal area represented by Douglas-fir in 2016 (A) and 2017 (B).

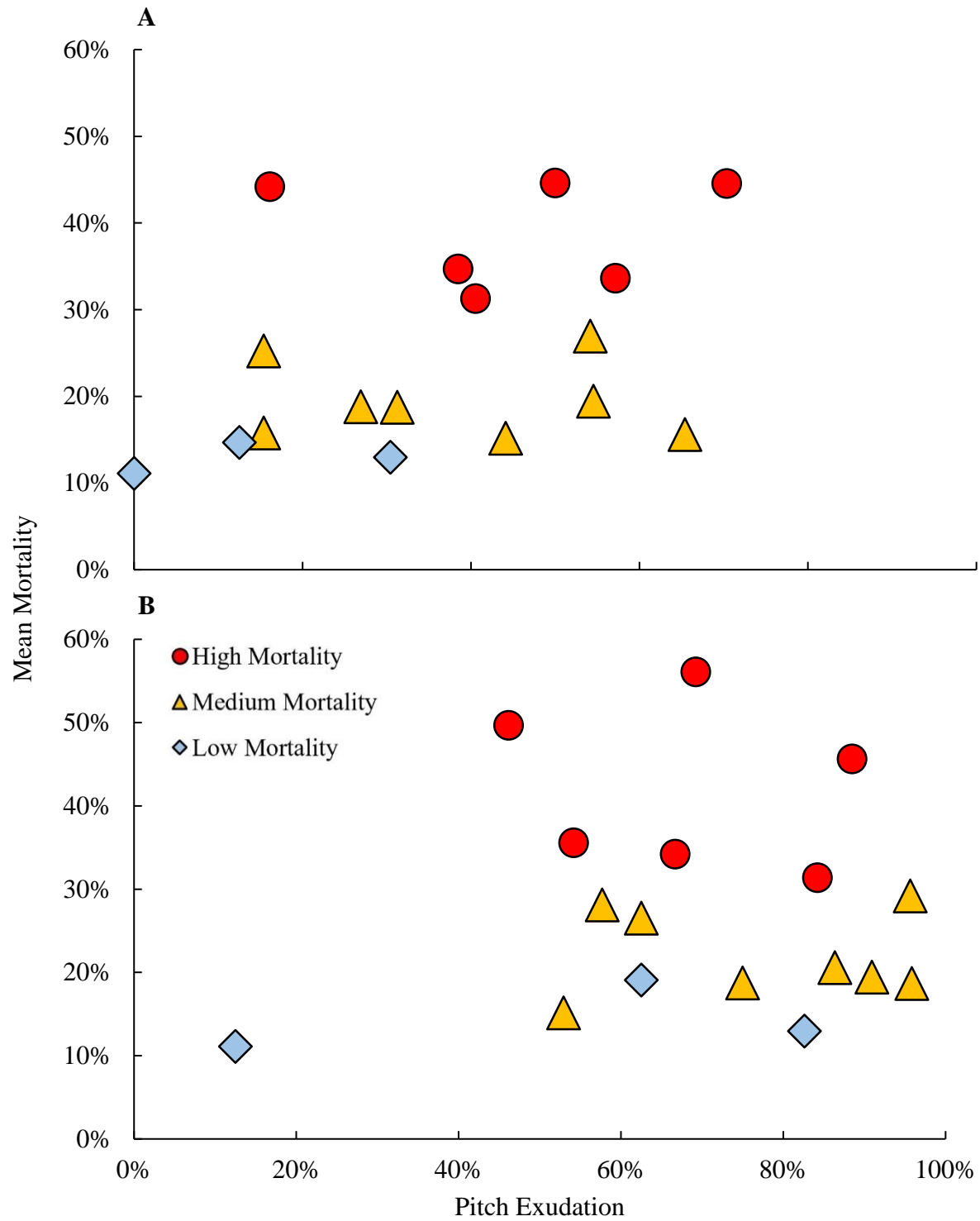


Figure 3.10. Mean percent of standing dead Douglas-fir for each mortality class by the percentage of Douglas-fir stems with medium-to-high (> ~33%) pitch exudation in 2016 (A) and 2017 (B).

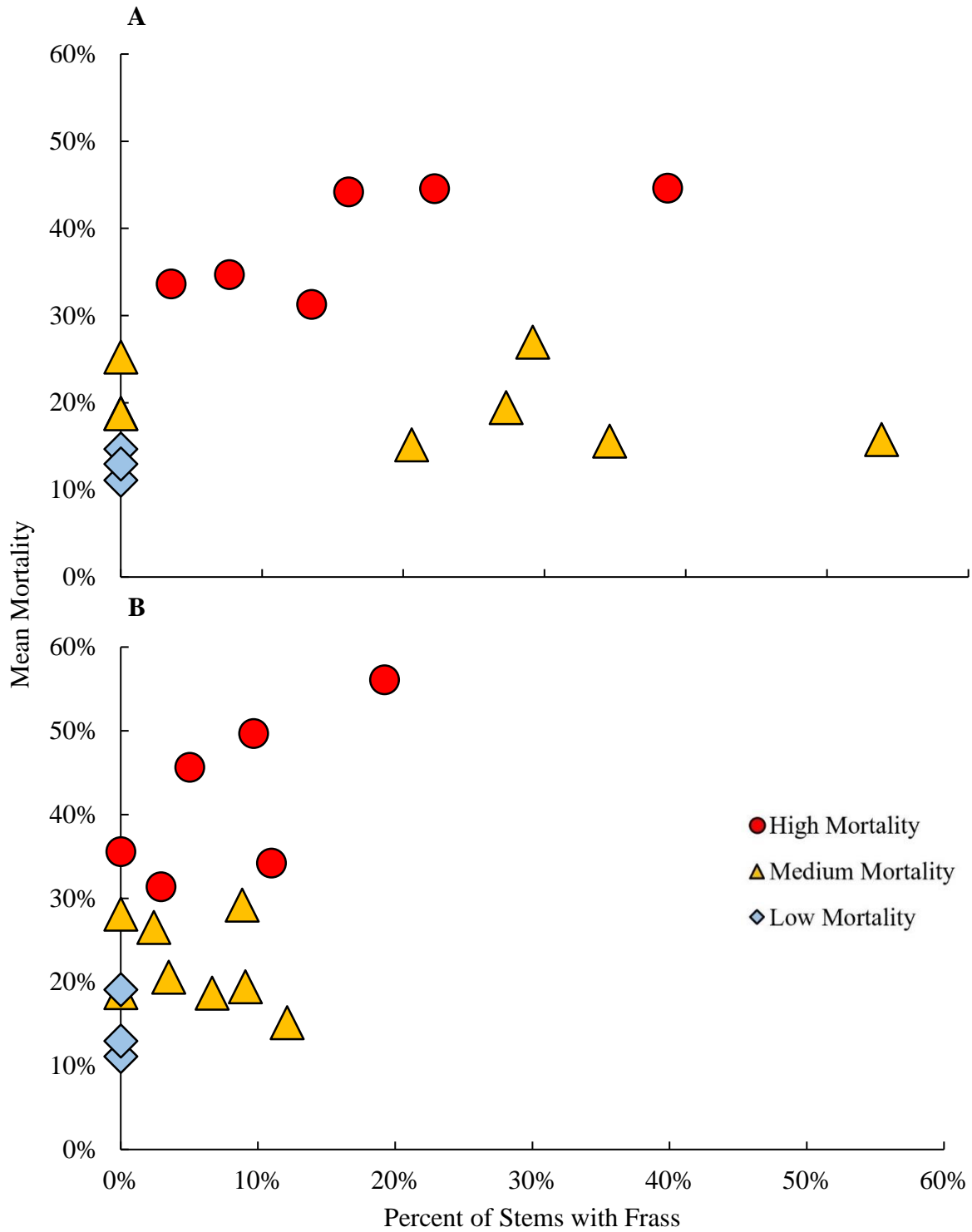


Figure 3.11. Mean percent of standing dead Douglas-fir for each mortality class by the percent of Douglas-fir stems with external Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) frass in 2016 (A) and 2017 (B).



Figure 3. 12. Mean percent of standing dead Douglas-fir for each mortality class by the percent of Douglas-fir stems with ground-level subdermal root rot mycelium (*Armillaria* spp.) in 2016 (A) and 2017 (B).

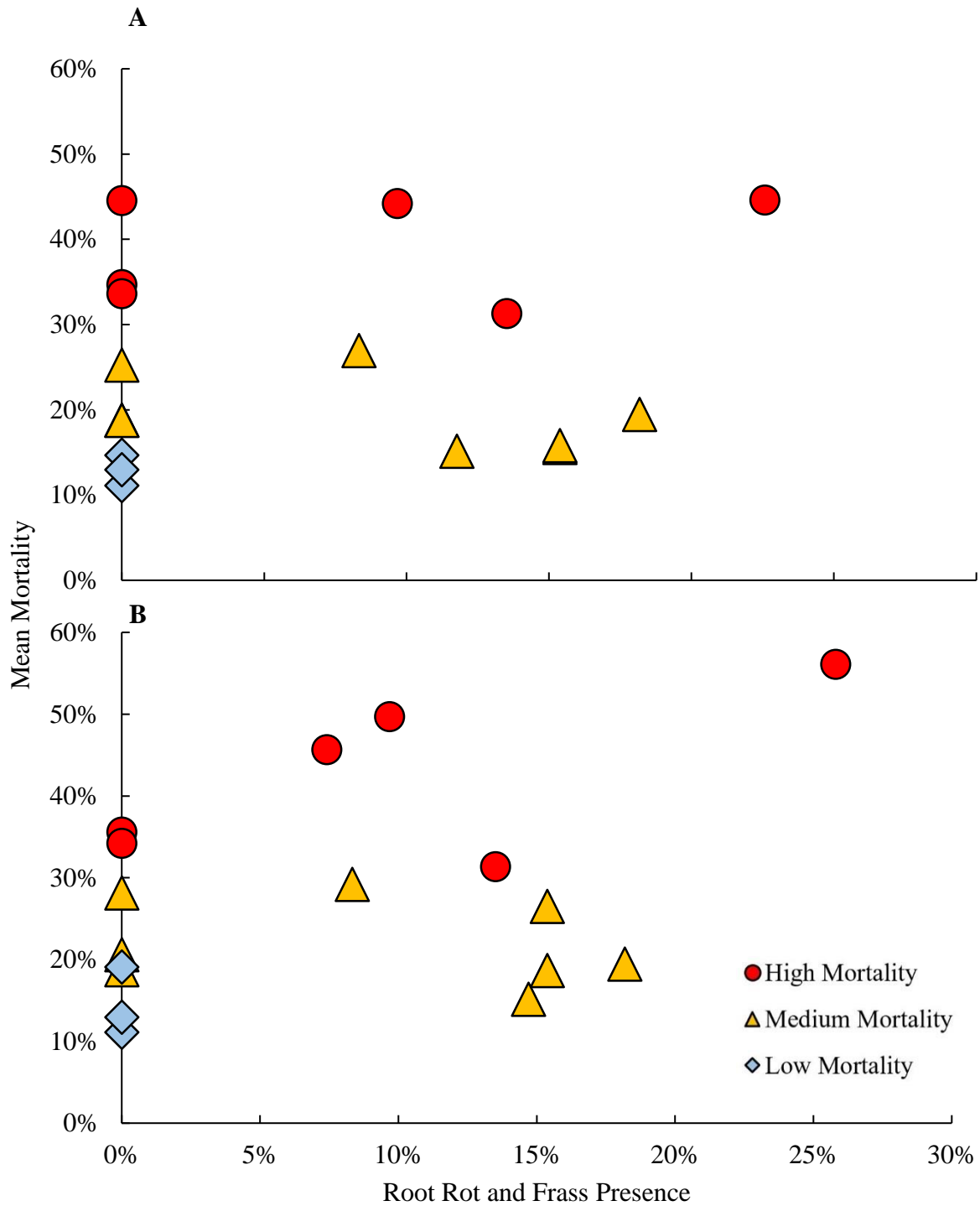


Figure 3.13. Mean percent of standing dead Douglas-fir for each mortality class by the percent of Douglas-fir stems with ground-level subdermal root rot mycelium (*Armillaria* spp.) and external Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) frass in 2016 (A) and 2017 (B).