

THESIS

ASSESSING THE EFFECTS OF ECOSYSTEM DISTURBANCE ON TWO INSECT VECTORS OF PINE WILT DISEASE IN THE SOUTHERN ROCKY MOUNTAINS

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ABSTRACT

ASSESSING THE EFFECTS OF ECOSYSTEM DISTURBANCE ON TWO INSECT VECTORS OF PINE WILT DISEASE IN THE SOUTHERN ROCKY MOUNTAINS

Ecosystem disturbances such as wildfire and bark beetle outbreak may structure the dynamics of forest tree diseases by altering vector behavior and population dynamics. As climate change intensifies, disturbances are increasing in both severity and intensity; however not all disturbance types have equivalent ecological effects: fire is abiotic and more homogenous in its spread, while bark beetle outbreaks are biotic and more spatially heterogeneous.

Monochamus beetles are disturbance specialists, colonizing recently burned or stressed trees, and are important vectors of pine wilt disease, a lethal vascular wilt of conifers caused by the pinewood nematode (*Bursaphelenchus xylophilus*). Although pine wilt disease is globally destructive, studying its dynamics in the native range provides insight into how disturbance regimes influence disease risk under future climate scenarios. I examined how two major disturbance types- wildfire and spruce beetle (*Dendroctonus rufipennis*) outbreak—affect vector infection frequency, flight phenology, and population patterns in *Monochamus clamator* and *M. scutellatus* across forests of Colorado.

In ponderosa pine forests impacted by recent wildfires, nematode infection prevalence in vectors was highest shortly after disturbance and declined over subsequent years. Infected individuals initiated flight earlier than uninfected beetles, and the

relationship between infection probability and distance from the burn perimeter differed between species, indicating species-specific spatial responses to fire. These results suggest that wildfire can create short-term post-disturbance windows of elevated pathogen transmission risk.

In contrast, in subalpine spruce–fir forests affected by spruce beetle outbreak, *M. scutellatus* abundance increased in outbreak stands, but infection probability and flight phenology did not differ between outbreak-affected and unaffected areas. Smaller beetle body size in outbreak stands suggests reduced host quality or increased competition, but infection dynamics remained stable across the disturbance gradient.

Together, these studies demonstrate that disturbance type matters: wildfire, an acute abiotic disturbance, can amplify vector infectivity over short timescales, whereas bark beetle outbreak, a slower, chronic, and more heterogeneous disturbance, does not. These findings emphasize the need to distinguish disturbance regimes when predicting disease risk and highlight the importance of incorporating disturbance history into forest disease monitoring and management.

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CHAPTER 1

SPECIES-SPECIFIC PATTERNS OF FLIGHT PHENOLOGY AND INFECTION RATES IN TWO INSECT VECTORS OF PINE WILT DISEASE FOLLOWING FOREST DISTURBANCE IN THE SOUTHERN ROCKY MOUNTAINS

1.1 Introduction

Vector-borne diseases require the interaction of a pathogen, host, and a vector, mediated by environmental conditions (Keesing et al. 2006). A changing climate is likely to have strong effects on the environmental conditions that affect transmission and severity of vector-borne diseases. For example, ecological disturbances such as wildfire, drought, and hurricanes, as well as anthropogenically mediated disturbances such as land use change and habitat fragmentation, are becoming more frequent and severe (Dale et al. 2001); (Stevens-Rumann et al. 2018); (Allen et al. 2010); (Shultz et al. 2005). Changing patterns of ecosystem disturbance can impact the transmission of arthropod-borne plant and animal diseases. For example, anthropogenically mediated disturbance such as urbanization and agriculture is linked to higher flea infestation in mammals, creating conditions favorable for flea-borne disease transmission (Friggens & Beier 2010) , while deforestation has increased malaria transmission risk in previously unsuitable areas (Lindblade et al. 2000). In forest ecosystems, wildfire interacts with insect-vectored pathogens as well as insects themselves, creating feedback loops that increase fuel load and susceptibility to subsequent disturbance (Ray et al. 2019). For example, fire can predispose surviving trees to bark beetle attack, which often facilitates colonization by

blue stain fungi (*Ophiostoma* spp.), reducing nutrient and water transport and accelerating tree mortality, thereby reinforcing disturbance driven feedback loops (Ray et al. 2019; Six & Wingfield 2011). Because forests experience multiple overlapping biotic and abiotic stressors, often acting synergistically, vulnerability to diseases is potentially increasing with global climate change (Allen et al. 2015), and the global movement of pathogens and pests (Roy et al. 2014) (Santini et al. 2013).

Although effects of ecosystem disturbance are well documented for human and animal diseases, they are far less understood for plant pathogens in forest ecosystems. Ecosystem disturbance can alter communities of insect vectors in species-specific ways (Loaiza et al., 2017). Wood-boring beetles in the genus *Monochamus* are disturbance specialists, often reaching high abundance in fire-damaged stands where volatiles and pyrolysis products signal host stress (Costello et al., 2011), which can attract beetles. Previous studies report that proximity to recent wildfire perimeters is associated with increased beetle abundance (Costello et al. 2011; Atkins et al. 2021). *Monochamus* beetles are xylophagous as larvae and create deep galleries in the sapwood until pupation, where the pupae can be colonized by nematodes (Jung et al. 2020). Newly emerged adults are attracted to stressed or recently dead conifers for oviposition, where larvae can successfully develop (Saint-Germain et al. 2004). However, before reproduction, adults must undergo a period of maturation feeding on the shoots and bark of living trees. It is during this feeding that *Monochamus* spp. can transmit nematodes, most notably *Bursaphelenchus xylophilus*, or the pine wood nematode (PWN), the causal agent of the lethal pine wilt disease (Vicente et al. 2012).

Pine wilt disease is a lethal vascular wilt of conifers that has no treatment and can cause rapid mortality, with visible symptoms present 15–20 days after infection. Globally, pine wilt disease is among the most serious biotic threats to coniferous forests, with projected losses exceeding \$1 billion annually in timber resources (Rutherford et al., 1990; Soliman et al., 2012; Atkins et al., 2021). The nematode is presumed to be native to North America, where many native forest conifers are resistant (Bowers et al., 1992; Atkins et al., 2021). In the southern Rocky Mountains, initial detections of pine wilt disease in the Front Range region of Colorado were made in nonnative Scots pine (*Pinus sylvestris*) in 2006 (Blunt et al., 2014), followed by the first description of symptomatic native ponderosa pine (*P. ponderosa*) in 2016 (Atkins et al., 2021). Ponderosa pine forests may act as reservoirs of infection and serve as transmission bridges to more susceptible urban landscapes (Atkins et al., 2021). Two *Monochamus* species (*M. clamator* and *M. scutellatus*) occur in Colorado and are vectors of pine wilt nematode, with about 4% of wild adult beetles testing positive for pine wilt nematode (Atkins et al. 2021). Although earlier work has shown that abundances of both beetle species can increase near recent wildfire perimeters (Costello et al. 2011; Atkins et al. 2021), the consequences of wildfires on the potential for transmission of pine wilt nematode (PWN) remain unclear. However, infected beetles may exhibit different behaviors and phenology than non-infected individuals, potentially affecting the probability of disease movement.

We aimed to study pine wilt disease in its native range and evaluate patterns of vector movement and infectivity across a geographic ‘distance to recent wildfire’ gradient to ask whether wildfire disturbance is potentially related to disease transmission

dynamics. Little is known about how wildfire influences beetle flight phenology or probability of infection across spatial gradients, or whether patterns of infectivity vary over time. To address this knowledge gap, we tested three hypotheses: (1) PWN infection status affects beetle flight phenology, (2) infection frequency in the population changes over time following wildfire disturbance, and (3) infection probability in vector populations is greater near fire perimeters and decreases with distance from fire. The research reported here provides insight into disturbance–disease interactions in forest ecosystems and their implications for forest health management in a changing environment.

1.2 Materials & Methods

This study was conducted in the lower montane forests of the Colorado Front Range, within Larimer and Boulder counties. The habitat is dominated by ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) stands. Other trees in the area include Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* Douglas ex Loudon), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), and quaking aspen (*Populus tremuloides* Michx.) Study sites consisted of two canyon systems: Cache La Poudre Canyon (Larimer County) and St. Vrain Canyon (Boulder County). These locations were selected to represent a gradient of distance to fire based on the occurrence of two large wildfires in 2020: the Cameron Peak Fire in Larimer County and the Calwood Fire in Boulder County (Figure 1.1). Although Colorado has a vast fire disturbance history, and older fires also occurred in the study area, we restricted our analysis to these recent, well-

documented events. Including multiple overlapping historical fires would have overcomplicated and confounded interpretation of distance effects, since stands may have been subject to repeated or mixed-severity disturbances, making it difficult to isolate the influence of any single fire. While burn severity is heterogenous within large wildfire perimeters, distance from the fire edge served as a consistent spatial proxy for disturbance intensity across sites. Patterns of live basal area across this gradient indicate lower live basal area (i.e., higher mortality) closer to the fire perimeter, supporting distance as a proxy for disturbance intensity (Figure 1.5). By focusing on the 2020 fires, we ensured consistency in disturbance age, allowing clearer inference about post fire infection dynamics. Fire perimeters were mapped in ArcGIS Pro using Monitoring Trends in Burn Severity (MTBS) data. Trap placement locations were selected first based on the mapped fire perimeters, and final trap placement selection was guided by field observations prioritizing accessible locations with intact ponderosa pine-dominated stands and visible fire damage for sites closer to the burn perimeter.

In each canyon, 10 traps were placed along a transect extending from the interior of the burn scar outward to unburned forest, capturing a gradient of distance from fire that ranged from 0 to 15 km from the burn perimeter. Trap elevations ranged from 1,730 to 2,615 m above sea level. Basic stand structure was assessed at each trap site to characterize forest conditions. Basal area of live and dead trees was measured using a variable-radius plot method with an angle gauge (Basal Area Factor = 20). At each site, counts were used to calculate mean basal area (ft^2/ha) of live trees and standing dead trees. The habitat at all

sites was predominately *Pinus ponderosa* forest with an average live basal area of 101m²/ha and dead basal area of 22m²/ha.

Trapping was conducted during three sampling seasons (2021, 2022, and 2024). In 2021, traps were deployed in both Cache La Poudre and St. Vrain Canyons (20 traps total). In 2022 and 2024, sampling was limited to Cache La Poudre Canyon due to access restrictions in St. Vrain Canyon (10 traps these years). At each selected trapping location, a Barnaby panel trap (Synergy Semiochemicals Corp., Delta, British Columbia, Canada) was deployed and secured to a sturdy *Pinus ponderosa* tree. Each trap was baited with a proprietary *Monochamus* lure (Synergy Semiochemicals Corp., item #3280) containing a blend of monochamol, ipsenol, α -pinene, and ethanol. A dichlorvos-based resin vapor strip was used to kill captured insects (Hot Shot No-Pest strip, Spectrum Brands, Middleton, WI, USA). Each strip was removed from its protective case and cut into ten pieces prior to deployment. Sites were sampled weekly over the duration of the *Monochamus* flight period from August through October (Atkins et al. 2021) in each sampling year. Each trap was collected for approximately eight weeks per season, resulting in ~ 2,240 total trap-days across all sampling years.

During each visit, beetles were removed from the collection cup and returned to the lab for identification and processing. Beetles were stored at -20 °C until processing. Individuals were identified to species and for each specimen sex and mass were determined. Detection of pine wood nematode (*Bursaphelenchus xylophilus*) was conducted using a proprietary loop-mediated isothermal amplification (LAMP) method and kit (Bx detection kit; Lot no. 39005D, Nippon Gene Co., Ltd., Tokyo, Japan). For DNA

extraction, each beetle was bisected longitudinally, and one half was ground to a fine powder in liquid nitrogen using a sterile mortar and pestle. The resulting tissue powder was transferred to individual microcentrifuge tubes, and extraction solution was added according to manufacturer specifications. LAMP reactions were performed with the extracted DNA following the manufacturer's instructions for pine wood nematode detection. All beetles were tested in this way for the presence or absences of PWN.

Data analysis

All analyses were performed in R version 4.5.0 (R Core Team, 2025). Unless otherwise stated, a Type I error rate of $\alpha = 0.05$ was used to determine statistical significance.

H1: Infected beetles have different flight phenology than uninfected beetles.

First, we fitted non-parametric logistic regression (NPLR) models to cumulative beetle captures over time using the `nplr` package in R (Commo & Bot, 2016). For each trap and each combination of species, infection status, and year, we extracted the ordinal dates corresponding to 10%, 50%, and 90% cumulative capture (after the methods described by Dell and Davis 2019). These thresholds were selected as a general representation of flight initiation, peak, and conclusion, respectively (Figure 1.2). Most flight phenology models provided strong fits to the data ($R^2 > 0.90$), though models that lacked sufficient data to produce reliable curves (less than 10 beetles) were excluded from further analyses.

We then tested for differences in flight timing between species and infection status using a two-way analysis of variance (ANOVA) on each of the three selected flight phenology thresholds (10%, 50%, and 90% capture dates). Species, infection status, and their interaction were included as fixed effects. The analysis was limited to data from 2021

and 2022, as infection rates in 2024 were extremely low (0.8% in *M. clamator* and 3.4% in *M. scutellatus*), preventing meaningful statistical comparison. Each trap was treated as an experimental unit. Assumptions of normality and homogeneity of variance were verified prior to interpretation using residual plots and Levene's test.

H2: Infection rates vary interannually.

Chi-square tests were used to analyze differences in infection rates (%) due to the effect of time since fire. Tests were conducted independently for each species across sampling years (2021, 2022, and 2024).

H3: The frequency of infected vectors varies with distance from recently burned areas.

To test this hypothesis, we used a generalized linear model (GLM, family=binomial) with infection status (infected/uninfected) as the binary response variable. Fixed predictors included species (*M. clamator* or *M. scutellatus*), years since fire, distance from the burn perimeter (km), and all possible 2- and 3-way interactions.

Years since fire was treated as a categorical factor so that infection probabilities could vary across sampling years. The full model was simplified using backward stepwise selection based on AIC, which retained species, years since fire, distance from fire, and the interaction terms species × years since fire and species × distance. This allowed us to test whether infection probability changed with time since fire or distance from burns, and whether those patterns differed between the two beetle species.

1.3 Results

Over the course of the study, a total of 1,455 adult *Monochamus* beetles were collected, including 1,128 *M. clamator* and 327 *M. scutellatus* (Table 1.1).

H1: Infected beetles have different flight phenology than uninfected beetles.

There were significant differences due to the effect of species on initiation of flight (10% cumulative capture); *M. clamator* flew significantly earlier than *M. scutellatus* ($F_{1,83} = 5.740$, $p = 0.019$). On average, *M. clamator* initiated flight 5.542 days earlier than *M. scutellatus* (233.750 ± 1.521 SE vs. 239.292 ± 2.691 SE). However, infection status had no effect on flight initiation ($p = 0.110$), nor was there evidence of a species \times infection status interaction ($p = 0.742$).

Both species and infection status significantly predicted variation in peak (50% cumulative capture) flight phenology (Species: $F_{1,104} = 2.114$, $p = 0.149$; Infection: $F_{1,104} = 10.877$, $p = 0.001$). However, there was no evidence of a species \times infection status interaction ($F_{1,104} = 1.235$, $p = 0.269$). Peak flight occurred earlier in infected beetles than uninfected beetles in both species. Infected *M. clamator* reached 50% capture at day 247.5 ± 2.2 SE compared to 253.7 ± 0.9 SE for uninfected ($\Delta = 6.2$ days). Similarly, infected *M. scutellatus* peaked at day 253.2 ± 3.6 SE as compared to day 255.3 ± 1.7 SE for uninfected individuals ($\Delta = 2.1$ days) (Figure 1.3).

Infection status had strong effects on variation in the conclusion of the flight period (90% cumulative capture; $F_{1,83} = 32.490$, $P < 0.001$), but there was no evidence of a species effect ($P = 0.767$) or species \times infection status interaction ($P = 0.603$). Infected beetles

consistently finished flight earlier than uninfected beetles, with infected *M. clamator* ending at day 258.8 ± 2.8 SE compared to 273.8 ± 1.4 SE for uninfected ($\Delta = -15.0$ days), and infected *M. scutellatus* ending at day 259.1 ± 4.3 SE compared to 271.5 ± 2.1 SE for uninfected ($\Delta = -12.4$ days).

H2: Infection rates vary interannually.

Infection frequency declined with time since fire, but patterns differed between species. In *M. clamator*, infection frequency varied strongly across years ($\chi^2 = 92.41$, $df = 2$, $p < 0.001$), dropping from 21.4% in 2021 to 4.9% in 2022 and 0.8% in 2024 (Figure 1.4). In contrast, infection rates in *M. scutellatus* did not differ significantly among years ($\chi^2 = 3.31$, $df = 2$, $p = 0.191$), but also showed a pattern of decline slightly from 9.8% in 2021 to 8.9% in 2022 and 3.4% in 2024.

H3: The frequency of infected vectors varies with distance from recently burned areas.

The probability of infection was influenced by both distance from fire and years since fire, with contrasting responses between species (Table 1.2). For *M. clamator*, the probability of infection increased with distance from fire ($\beta = 0.072$, $P < 0.001$) and declined strongly by 2024 ($\beta = -3.65$, $P < 0.001$). In *M. scutellatus*, the opposite pattern was detected: probability of infection decreased with distance from fire ($\beta = -0.198$, $P = 0.002$; Figure 1.5). Year effects were species specific, with *M. scutellatus* showing higher infection probability in 2022 and 2024 to *M. clamator*. Among predictors, years since fire was the strongest driver of infection probability, followed by distance to fire (Table 1.2).

1.4 Discussion

This study demonstrates that recent wildfire disturbance influences pine wilt disease dynamics in Colorado forests, with frequencies of beetle infection varying between vector species, with time since fire, and with the distance to a large wildfire disturbance. To our knowledge, this is the first study to show that wildfire can potentially affect transmission dynamics of a plant pathogen. For insect-vectored pathogens, ecosystem disturbance is consistently linked to elevated insect vector abundance and an increased risk of pathogen transmission. For example, outbreaks of malaria and dengue have been observed following hurricanes, floods, and deforestation; these disturbances create environmental conditions (such as increased standing surface water) that can favor vector population growth, and subsequent transmission opportunities expand (Shultz et al., 2005; Lindblade et al., 2000). In western North America, exposure to fires and drought may weaken tree defenses and create locally favorable conditions for colonization by *Monochamus* beetles, which are well-known disturbance specialists and are previously recorded orienting to recently burned stands (Costello et al. 2011; Atkins et al. 2020). Our analyses suggest that these patterns may have consequences for the epidemiology of globally-important plant diseases such as pine wilt under a trajectory of continued climate warming accompanied by a predicted increase in wildfire frequency and severity (Stevens-Rumann et al. 2018; Allen et al., 2010).

Pinewood nematode infection was associated with earlier peak flight phenology in both *Monochamus* species, suggesting that infection status alters beetle activity windows

and may increase opportunities for early-season transmission. The physiological mechanisms underlying this pattern are unknown, but merit further study. Nematodes colonize *Monochamus* beetles during pupation and reside primarily in the tracheal system and spiracles, and are transmitted through wounds created during early-season maturation feeding (Vicente et al. 2013), and transmission rates of PWN are typically highest between 2-4 weeks after emergence (Linit 1990). This parallels our finding that infected beetles have earlier peak flight timing but there was no statistical difference in flight initiation timing between infected and uninfected beetles. Nematode colonization could plausibly alter flight phenology transmission directly through physiological manipulation of *Monochamus* beetles or indirectly via the manifestation of stress in host trees.

Such mechanisms are described in other insect-vectored pathosystems. For instance, malaria parasites manipulate mosquito physiology directly by suppressing feeding until parasites mature and then increase biting behaviors once vectors are infectious (Cator et al. 2012). On the other hand, various plant pathogens indirectly manipulate vector behavior by altering the volatile profiles of host plants. *Bean pod mottle virus* makes soybean plants more attractive to Mexican bean beetles (*Epilachna varivestis*), changing feeding preferences in a way that increases spread to healthy plants (Smith et al. 2017). Similarly, *cucumber mosaic virus* induces a “pull-push” effect in aphids, altering probing patterns and dispersal to maximize early transmission by attracting uninfected aphids to infected plants, and then upon virus acquisition aphids subsequently prefer uninfected plants (Carmo-Sousa et al. 2014; Eigenbrode et al. 2018). It is possible that pinewood nematode has both direct physiological and indirect host-mediated effects on

Monochamus beetles: nematodes are often found abundantly in beetle spiracles (Mamiya & Enda, 1972; Vicente et al. 2013), which may induce early movement (flight and feeding) in order to maintain adequate oxygen levels. However, recently burned trees also exhibit starkly different volatile profiles than undamaged individuals (Costello et al. 2011), which could influence the settling and feeding preferences of infected or uninfected beetles.

In addition, infection prevalence in *Monochamus* beetles was considerably higher in the year immediately following fire and declined in following years, particularly in *M. clamator*, consistent with the hypothesis that recently disturbed stands provide favorable conditions for pathogen persistence and transmission. This pattern also corresponded to overall *Monochamus* abundance: trap capture abundance in 2022 and 2024 declined by 33 and 47%, respectively, in comparison to 2021 trap captures. However, the drivers of this change are not yet clear. Freshly disturbed stands attract a suite of disturbance specialist coleoptera, including *Monochamus* spp., and these communities shift rapidly after disturbance as stands recover (Saint-Germain et al. 2004). It is possible that immediately following wildfire disturbance elevated host tree stress creates a window of susceptibility during which infection frequency peaks, but as conditions stabilize, both populations and infection rates decline. If true, this could manifest as increased disease prevalence in forest trees in the year following wildfire, though we did not evaluate tree infection status here. Similar patterns of elevated insect vector infectivity following natural disturbances are described in both animal and plant pathosystems. For instance, mosquito abundance and outbreaks of malaria and Zika virus peak within six months immediately following hurricanes (Waddell et al. 2021). Likewise, armillaria root disease infection frequency often

increases immediately after logging or fire when stumps and stressed trees provide entry points, and then infection rates diminish as regeneration progresses (Shaw and Kile, 1991). In the present study, vector (*Monochamus*) abundances and infection rates declined substantially by two- and four-years post-disturbance, suggesting that pine wilt disease management efforts may be the most impactful in the growing season immediately following wildfire.

Our data show that responses of infection probability relative to distance from fire perimeters was species-specific. *Monochamus clamator* showed higher infection further from the wildfire perimeter, while *M. scutellatus* exhibited the opposite pattern, with higher rates of infection closer to the fire perimeter. These contrasting patterns suggest that disturbance does not create a uniform disease landscape but instead produces species-specific spatial risk zones. Previous work has shown that *Monochamus* abundance is often linked to fire footprints (Costello et al. 2011, Atkins et al. 2020), but until now no studies have explicitly assessed spatial gradients of nematode infection relative to burn perimeters. Our findings parallel broader evidence from tropical disease systems, where disturbance reorganizes vector communities in species-specific ways. Loaiza et al. (2017) demonstrated that disturbance reshaped mosquito community structure along a gradient of forest disturbance. Colonist species thrived in disturbed habitats and were more likely to transmit pathogens, while climax species declined in altered landscapes. Here, even closely related sympatric *Monochamus* species diverged in their relationship with disturbance, underscoring the potential need for species-targeted management strategies. Areas near burns may be at greater risk from *M. scutellatus*, while stands that are more

distant may face a higher risk of secondary biotic disturbance from *M. clamator*. This could narrow the scope of target species management.

While this study provides novel insights into how wildfire influence pine wilt disease dynamics, some limitations of our study should be considered when interpreting our results. First, Colorado has a long history of wildfire and fire history on the landscape may complicate interpretation of spatial patterns. Our study considered fire perimeters of two large fires that occurred during 2020, however some of the traps further from the Cameron Peak burn perimeter were located within an older burn perimeter from the High Park fire of 2012 (Figure 1.1). Although we demonstrated that beetle infection decreases with time since fire, this fire history could still be influencing beetle distributions or infection dynamics and poses the question of if certain species might be more attracted to older fires. There was also an elevational gradient coincident with the distance gradient that should be considered. Second, our analysis is based on the prevalence of infected vectors rather than direct measurements of pathogen transmission to host trees. While infection status in beetles is a precursor to spreading disease, it does not capture the entire epidemiological story and linking vector infection to realized transmission in trees would benefit future studies. Although our models revealed contrasting species-specific associations with distance from fire, but these relationships may be shaped by legacy effects of past disturbances or unmeasured environmental or species-specific variables such as the different elevational requirements of *M. clamator* and *M. scutellatus*. Together, these factors point toward important directions for future research.

This study demonstrates that wildfire disturbance structures the dynamics of an insect-vectored pathogen, linking PWN prevalence in *Monochamus* beetles to time since fire, distance from wildfire perimeter, and flight phenology. By showing that infection risk is highest immediately following disturbance, that infected beetles have an earlier flight phenology, and that species respond differently to disturbance across spatial gradients, our findings highlight wildfire as a critical driver of vector-pathogen interactions in forests. These results align with broader disturbance-disease theory (Ayres and Lombardero, 2000; Seidl et al., 2017; Allen et al., 2010) and suggest that post fire conditions may temporarily increase opportunities for pine wilt disease transmission. However, future studies should verify this with sampling from host trees, in addition to vector populations. From a management perspective, our work indicates that trapping and monitoring efforts should be prioritized earlier in the season and directly after disturbance when infection frequency is highest in vector populations, and that vector management strategies should be species-specific, narrowing the scope of species management to focus on *M.scutellatus* near disturbance, and *M.clamator* at further distances from disturbance. Together, these findings underscore the importance of integrating both disturbance history and vector ecology into forest health planning, with implications for predicting pine wilt disease risk not only in Colorado but also in other fire-prone ecosystems worldwide.

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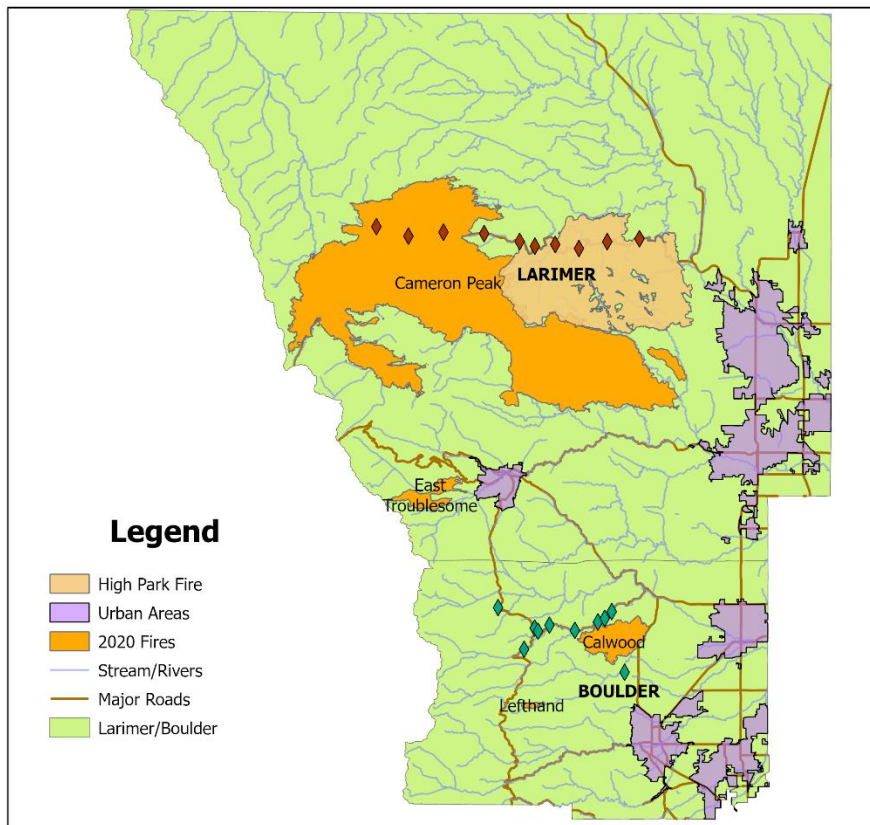
Table 1.1 A summary of beetle captures and infection frequencies by species, year, and site.

Year	Site	Species (infection rate)	
		<i>M. clamator</i>	<i>M. scutellatus</i>
2021	Poudre Canyon	235 (29.8%)	35 (11.4 %)
	St. Vrain Canyon	298 (14.8%)	88 (9.1%)
2022	Poudre Canyon	325 (4.9%)	112 (8.9%)
2024	Poudre Canyon	261 (0.8%)	89 (3.4 %)

Table 1.2 Generalized linear model results for probability of pinewood nematode infection status in *Monochamus* beetles as a function of species, distance from fire, and years since fire (GLM, binomial family). Significant species × distance and species × year interactions indicate contrasting infection patterns between *M. clamator* and *M. scutellatus*.

Parameter	Estimate (β)	SE	Z-value	P
Intercept (M. clamator, 1 year post-fire)	-1.753	0.173	-10.121	<0.001
Species (M. scutellatus)	-0.145	0.372	-0.391	0.696
Years since fire (2 years, M. clamator)	-1.702	0.280	-6.088	<0.001
Years since fire (4 years, M. clamator)	-3.654	0.719	-5.081	<0.001
Distance from fire (km, M. clamator)	0.072	0.020	3.527	<0.001
Species × 2 years (M. scutellatus)	1.647	0.533	3.091	0.002
Species × 4 years (M. scutellatus)	2.631	0.980	2.685	0.007
Species × Distance (M. scutellatus)	-0.198	0.065	-3.068	0.002

Colorado Wildfires and Study Sites in Larimer and Boulder Counties



5 2.5 0 5 10 15 20 Miles

Data: MTBS Fire Perimeters
 Projection: NAD 1983 UTM
 Zone 13N
 Map by: Hailee Nolan, CSU

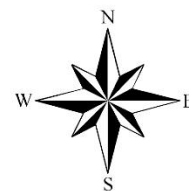
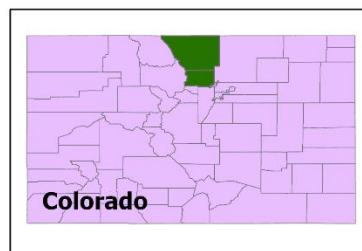


Figure 1.1 2020 wildfires, and trap locations within Larimer and Boulder counties.

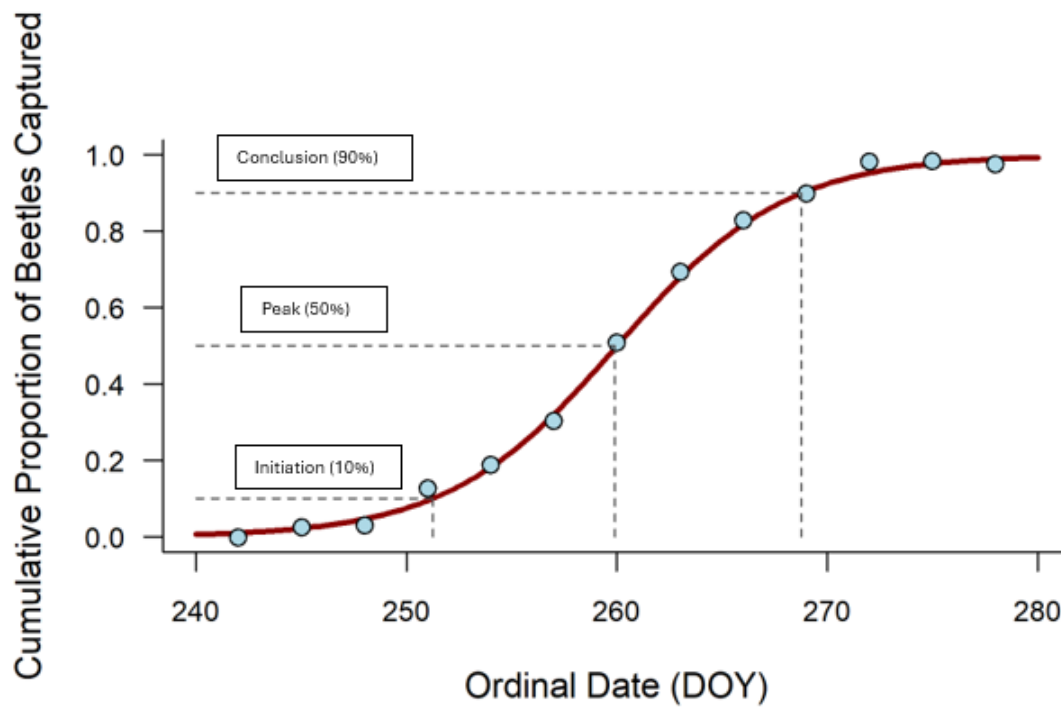


Figure 1.2 Example NPLR cumulative capture curve illustrating how 10%, 50%, and 90% capture dates (Day Of Year) are derived. Dashed horizontal lines mark cumulative thresholds; dashed vertical lines indicate the corresponding DOY at the curve intersections.

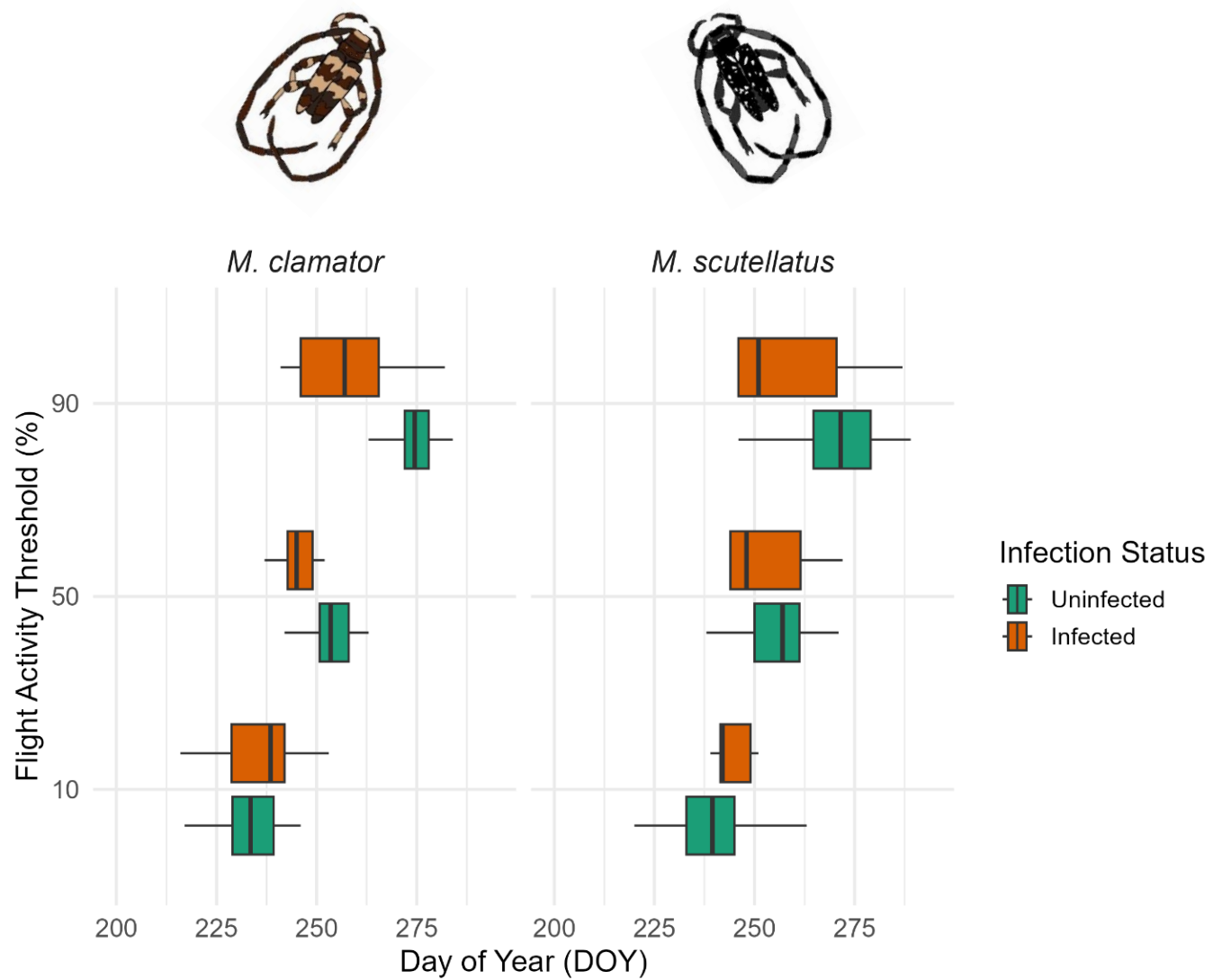


Figure 1.3 Boxplots of flight timing for *Monochamus clamator* and *Monochamus scutellatus* based on trap-level estimates of the ordinal day at which 10%, 50%, and 90% cumulative captures were reached in 2021 and 2022.

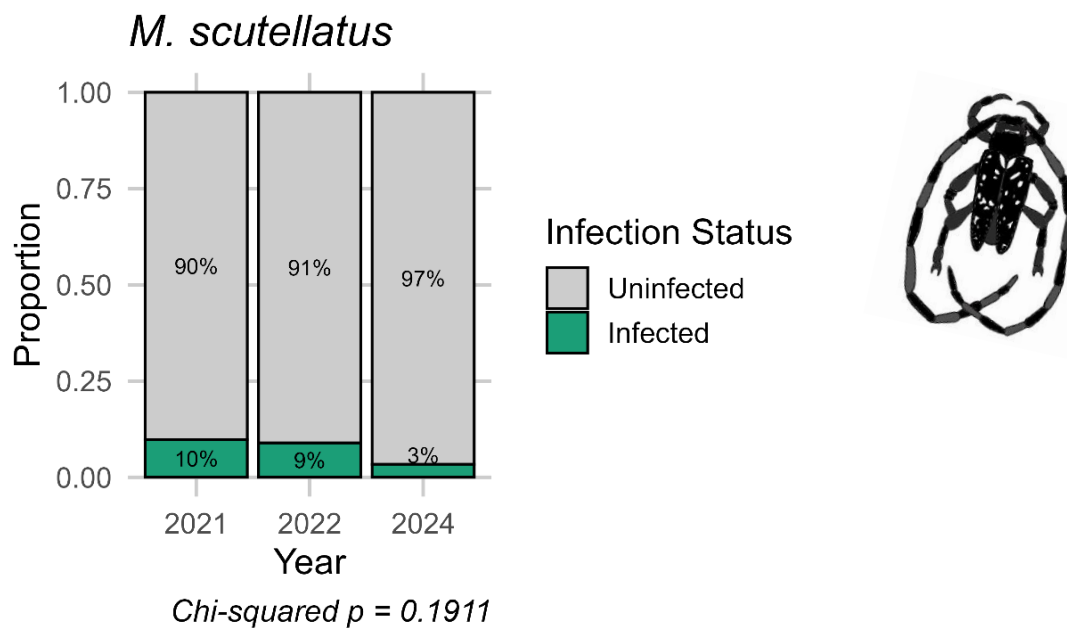
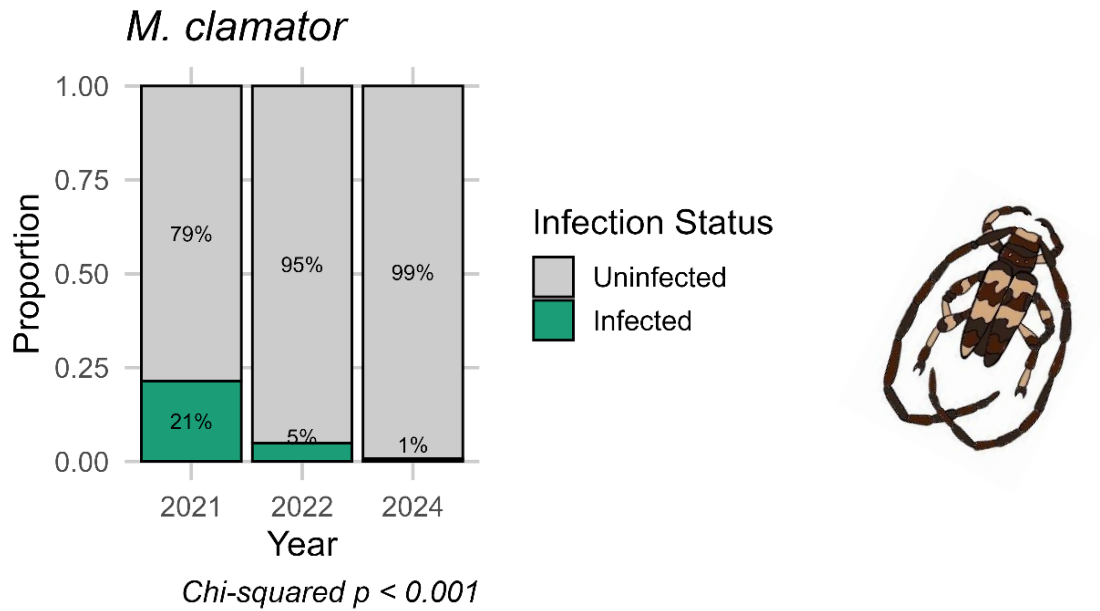


Figure 1.4 Variation in infection rates of *M. clamator* (top panel) and *M. scutellatus* (bottom panel) at one, two, and four years since fire. Bars show proportions of beetles infected with pinewood nematode (gray = uninfected).

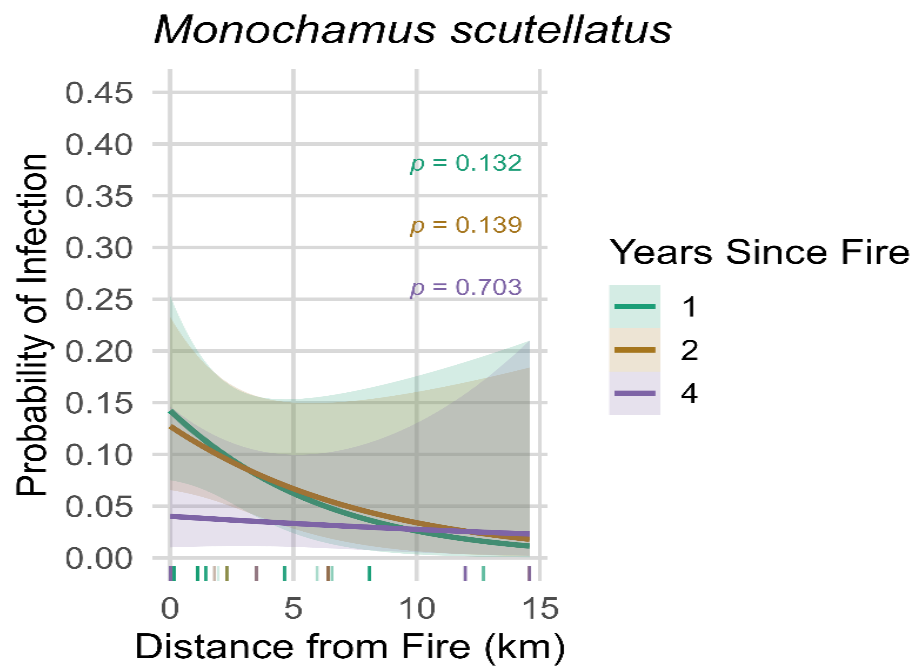
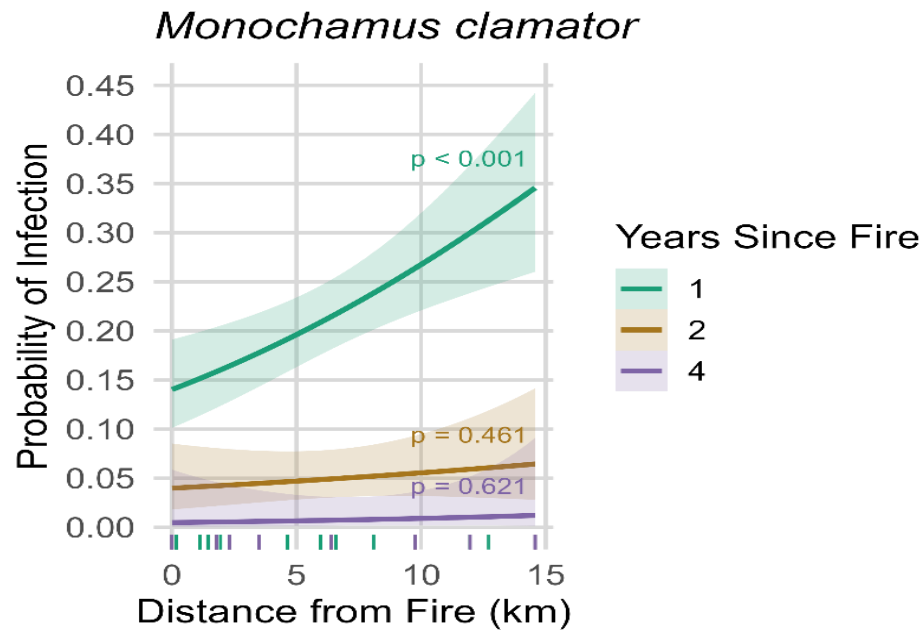


Figure 1.5 Model effects estimates showing the probability of infection in relation to distance from fire for *Monochamus clamator* (top) and *M. scutellatus* (bottom). Gray shading indicates 95% confidence intervals. Tick marks along the x-axis indicate the distances of trap locations where beetles were collected.

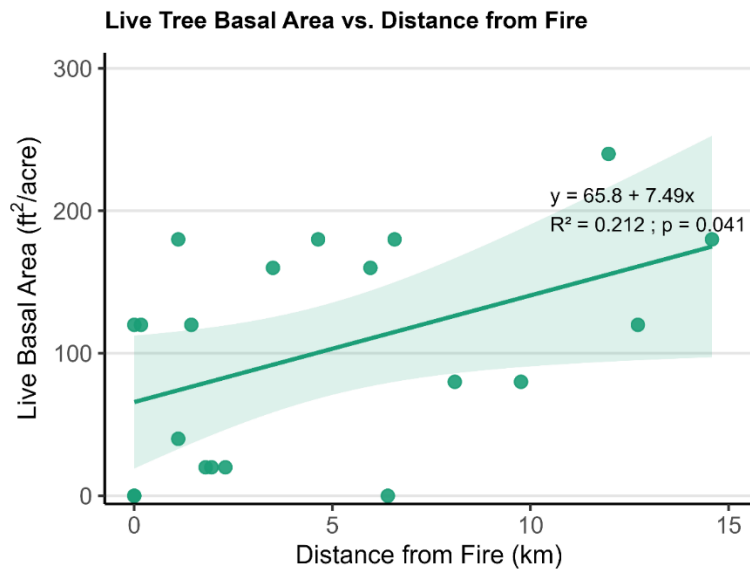


Figure 1.6 Basic linear regression showing that as distance from fire increases, live basal area increases. Traps closer to the burn perimeter had smaller live basal area and higher dead basal area.

CHAPTER 2

DISTURBANCE TYPE MATTERS: SPRUCE BEETLE OUTBREAKS DO NOT ALTER PINE WILT DISEASE DYNAMICS IN COLORADO SUBALPINE FORESTS

2.1 Introduction

Forest disease dynamics are shaped by interactions among hosts, vectors, pathogens, and disturbance, with climate change amplifying the frequency and severity of natural ecosystem disturbances including wildfires and bark beetle outbreaks (Allen et al. 2010; Ayres & Lombardero 2000). Such disturbances may elevate the risk of vector-borne diseases vis-à-vis increased stress on hosts and effects on vector population dynamics (Chaves & Koenraadt 2010; Loaiza et al. 2017). For example, in animal disease systems hurricanes and deforestation have indirectly increased malaria and dengue transmission even in previously unsuitable areas by increasing suitable habitat for vector mosquito populations (Lindblade et al. 2000; Shultz et al. 2005). In forests, disturbance alters both habitat suitability for insect species and may have similar indirect effects on plant (tree) pathogens, especially if drought and/or heat stress weaken tree defenses and create temporary windows of host susceptibility (Allen et al. 2010). Insect vectors of plant pathogens are known to have species-specific relationships with disturbance (Lindblade et al. 2000, Chapter 1); for example, beetles in the genus *Monochamus* are disturbance specialists in the southern Rocky Mountains and often reach high abundance after wildfire (Costello et al. 2011; Atkins et al. 2020).

Monochamus species play an important role in forest systems following disturbances. Through larval tunneling and consumption of tree tissues they contribute to decomposition, nutrient cycling, and forest succession (Costello et al. 2011). In most instances, *Monochamus* beetles are not considered pest species, and are often predatory on pest insects such as bark beetles (Schoeller et al. 2012). However, *Monochamus* species also serve as vectors of the pine wilt disease, a lethal vascular wilt caused by the pinewood nematode (PWN, *Bursaphelenchus xylophilus*). Globally, pine wilt disease is one of the most serious biotic threats to coniferous forests, affecting forests in many temperate and mediterranean climates across Europe and Asia, with projected annual timber losses exceeding \$1 billion (Vicente et al. 2012; Soliman et al. 2012). Although many North American pine species are resistant, recent detections of pine wilt in Colorado in forest habitats—including symptomatic ponderosa pine (*Pinus ponderosa*)—highlight its potential impact in the southern Rockies (Blunt et al. 2014; Atkins et al. 2021).

Monochamus are regularly reported colonizing fire-damaged trees, but studies have also shown that they are attracted to stands disturbed by windthrow, timber harvesting, and bark beetle outbreaks (Allison et al. 2000; Breton et al. 2013; Ray et al. 2019). Previous work in Chapter 1 demonstrated that wildfire disturbance influences infection rates of PWN in *Monochamus* spp. Here, we ask whether similar patterns emerge in stands affected by bark beetle outbreaks.

In Colorado, spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks have occurred during the past decade, causing widespread Engelmann spruce (*Picea engelmannii*) mortality (Hart et al. 2014) in subalpine forests. The spruce beetle is one of

the most significant agents of biological disturbance in North America, and during outbreaks beetle populations are capable of killing over 90% of mature spruce within stands (DeRose & Long, 2007). Spruce beetles kill trees through pheromone-coordinated mass attack of the phloem, overwhelming host defenses and disrupting water and nutrient transport (Schmid & Frye 1977). From 2000 to 2022, spruce beetle has cumulatively impacted nearly 1.9 million acres of Engelmann spruce forest in Colorado, representing over 40% of spruce-fir forests, making spruce beetle one of the most damaging bark beetle in the state (CSFS 2022), in addition to the mountain pine beetle which impacted 3.5 million acres between 1996 and 2013, or about 80% of the pine forests in Colorado (Negron et al. 2020; USDA Forest Health Highlights, 2022). Outbreaks are often triggered by events that weaken host defenses- especially drought, avalanches, windthrow events, and stand infestation with mistletoes (Christiansen et al. 1987). These conditions can result in the rapid buildup of endemic beetle populations in weakened or recently dead hosts, and then large populations begin attacking healthy, mature trees. In a recent regional study, Hart et al. (2014) found that outbreak severity varied depending on prior disturbance history and forest structure. While spruce beetle outbreak can be incited by prior disturbances, it is unknown whether spruce beetle outbreaks facilitate the secondary spread of pathogens following outbreak.

The overlap between bark beetle outbreaks and *Monochamus* host selection provides a unique opportunity to test whether one biotic disturbance may influence the secondary biotic disturbances of plant pathogens. *Dendroctonus* bark beetles are often the primary cause of tree mortality, while *Monochamus* spp. are secondary species that

typically colonize weakened hosts (Ray et al. 2019). Although *Monochamus* are known to respond to wildfire disturbance, they are attracted to volatiles such as ethanol and monoterpenes released by stressed trees (Costello et al. 2011). Attraction to hosts is further synergized by bark beetle pheromones, which *Monochamus* may use as kairomones during host selection (Costello et al. 2008; Allison et al. 2000). Population responses have been shown to be similar across fire and bark beetle disturbance, suggesting that *Monochamus* respond broadly to stress-related volatiles (Ray et al. 2019). Because both *Monochamus* and bark beetles both occupy the sapwood and consume phloem, resource overlap could lead to larval competition (Schoeller et al. 2012) or predation. Gut content analysis revealed *Monochamus titillator* larvae containing *Dendroctonus frontalis* DNA (Schoeller et al. 2012), indicating a predatory relationship. Thus, spruce beetle outbreaks may not only create resources for *Monochamus* larvae by weakening host trees, but could also indirectly alter pine wilt disease dynamics through competitive or facilitative interactions. To evaluate this possibility, I tested four hypotheses: (1) *Monochamus* abundance is higher within the perimeter of stands that experienced significant overstory mortality from spruce; (2) stand condition (spruce beetle affected vs. nonaffected control stands) and proximity to outbreak predict infection likelihood; (3) beetle mass differs by sex, infection status, and outbreak presence; and (4) infected beetles differ in flight phenology from uninfected beetles.

2.2 Materials & Methods

This study was conducted in the subalpine forests of the southern Rocky Mountains of Colorado, within Larimer, Jackson, and Clear Creek counties. The habitat is dominated by Englemann spruce (*Picea engelmannii* Parry ex Engelm.), blue spruce (*Picea pungens* Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and quaking aspen (*Populus tremuloides* Michx.), and also contains lodgepole pine (*Pinus contorta* Douglas ex Loudon) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Study sites consisted of two mountain passes: Cameron Pass in Larimer and Jackson counties, and Guanella Pass in Clear Creek County. These locations were selected based on the presence of spruce beetle (*Dendroctonus rufipennis*) kill from 2018-2023.

Spruce beetle affected areas were mapped in ArcGIS Pro using available polygons from the U.S. Forest Service National Insect and Disease Risk Map (NIDRM) (USFS Forest Health Protection, 2023). Fire perimeters from recent wildfires in the area were also mapped in ArcGIS Pro using Monitoring Trends in Burn Severity (MTBS) data to avoid confounding effects from known associations between *Monochamus* beetles and wildfire (Atkins et al., 2020; Costello et al. 2013). After mapping fire perimeters, we established an exclusion buffer of 500 m around the perimeters. This buffer distance was chosen based on published adult *Monochamus* maximum dispersal distances in field based studies (Torres-Vila et al. 2014; Togashi 1988), with the goal of placing traps beyond fire attraction zones. Preliminary trap placement locations were selected within areas affected and unaffected by spruce beetle kill and only in areas that fell outside of buffered fire perimeters. Ten trap locations were chosen within spruce beetle kill affected areas, and ten

trap locations were chosen in proximal unaffected areas. Final site selection was guided by field observations that prioritized accessible locations with or without obvious spruce beetle kill, and outside of burned areas (Figure 2.1). Trapping locations were divided evenly between study sites (i.e., each mountain pass had n=10 trap locations with n=5 locations within spruce beetle- affected areas and 5 outside of affected areas. Distances of each trap to the nearest bark beetle polygon ranged from 0 m (i.e., within affected stands) to 1732.5 m. All traps placed outside of spruce beetle affected areas followed the same 500 m buffer rule that was considered with burned areas. Basic stand structure was assessed at each trap location to characterize forest conditions. Basal area of live and dead trees was measured using variable-radius plots with an angle gauge (Basal Area Factor = 20). At each trapping location, counts were used to calculate mean basal area (ft²/ha) of live trees and standing dead trees, as well as the percentage of dead trees at each trapping location. The forest cover at all sites was predominantly spruce/fir forest with an average live basal area of 186.5 ft²/m for Cameron Pass and 212 ft²/m for Guanella Pass.

At each selected trapping location, a Barnaby panel trap (Synergy Semiochemicals Corp., Delta, British Columbia, Canada) was deployed and hung to the branch of a sturdy spruce or fir tree. Each trap was baited with a *Monochamus* lure (Synergy Semiochemicals Corp., item #3280) containing a proprietary blend of monochamol, ipsenol, α -pinene, and ethanol. A dichlorvos-based resin vapor strip was used to kill captured insects (Hot Shot No-Pest strip, Spectrum Brands, Middleton, WI, USA). Each strip was removed from its protective case and cut into ten pieces prior to deployment. Trapping was conducted in the summer of 2024, and traps were collected biweekly over the duration of the *Monochamus*

scutellatus flight period from July to August. This timing was chosen based on the data presented in Atkins et al. 2021. Each trap was collected for approximately 6 weeks, resulting in 840 trapping days (20 traps × 42 days). During each collection, beetles were removed from the collection cup, bagged and placed on ice, and returned to the lab for storage (−20 °C freezer), identification, and processing.

Individuals were identified to species and for each specimen sex and mass were also determined. Detection of pine wood nematode (*Bursaphelenchus xylophilus*) was conducted by the loop-mediated isothermal amplification (LAMP) method using a commercial nematode detection kit (Bx detection kit; Lot no. 39005D, Nippon Gene Co., Ltd., Tokyo, Japan). For DNA extraction, each beetle was bisected longitudinally, and one half was ground to a fine powder in liquid nitrogen using a sterile mortar and pestle. The resulting tissue powder was transferred to individual microcentrifuge tubes, and extraction solution was added according to manufacturer specifications. LAMP reactions were performed with the extracted DNA following the manufacturer's instructions for pine wood nematode detection. All collected beetles were tested in this way for the presence or absence of PWN.

Data analysis:

All analyses were performed in R programming environment, version 4.5.0 (R Core Team, 2025). A Type I error rate of $\alpha = 0.05$ was used to assign statistical significance.

H1: Beetle abundance of infected and uninfected beetles is higher inside of bark beetle affected stands.

We tested this hypothesis using a two-way ANOVA treating beetle count as the response variable and stand condition (spruce beetle kill or unaffected control stand), beetle infection status (presence/absence of pinewood nematode), and their interaction as fixed effects. Assumptions of homogeneity of variance were checked with Levene's test and were satisfied. Normality was assessed with the Shapiro–Wilk test and was not satisfied, so we also fit a generalized linear model with a Poisson distribution, using the same predictors and their interaction term.

H2: Tree mortality and proximity to bark beetle-kill predict infection likelihood.

We tested whether infection status of *Monochamus* beetles (infected vs. uninfected with pinewood nematode) was related to stand condition and distance from bark-beetle-killed trees. A generalized linear model (family=binomial) was used, treating infection status as the binary response variable and percentage of dead basal area, distance (m) from bark beetle-affected stands, and beetle sex (male or female) as predictor variables. Prior to evaluating this model we first verified that overstory basal area mortality was related to stand condition (i.e., spruce beetle-killed vs. unaffected control stands; Figure 2.2). Because logistic regression models estimate effects on the log-odds of infection, we converted coefficients into odds ratios for easier interpretation.

H3: Beetle mass differs by sex, infection status, and stand condition.

We tested whether *Monochamus* body mass differed by sex, infection status, and bark beetle activity using a generalized linear model (family=Gaussian). Beetle dry mass (g) was the response variable, with sex, beetle infection status (infected/uninfected), and stand condition as predictors. The full model included all main effects and their interactions:

(weight ~ sex * infection status * stand condition). Model assumptions were assessed prior to interpretation. Homogeneity of variance was evaluated using Levene's test, which was satisfied. Normality was tested with the Shapiro–Wilk test, which was not satisfied. To further evaluate this assumption, we examined a histogram of beetle mass values, which showed a slight right skew but no extreme deviations. Because linear models are reasonably tolerant to mild skewness (cite), particularly with larger sample sizes, we proceeded with the analysis using the linear model.

H4: Infected beetles exhibit a different flight phenology than uninfected beetles.

To assess whether infection status influenced flight phenology, we plotted cumulative flight activity curves of infected and uninfected beetles across all sites and sampling dates. We used the *nplr* package in R to fit non-parametric logistic regression curves of cumulative beetle captures (as described in Atkins et al. 2021), allowing visualization of potential shifts in the timing of peak flight between groups.

2.3 Results

During this study a total of 655 *M. scutellatus* were captured; 70 (10.6%) of beetles tested positive for PWN.

Our ANOVA test found that uninfected beetle abundance was 63% higher inside spruce-beetle affected stands than in unaffected stands, but the difference was not statistically significant. Infection status had a strong effect on beetle abundance, with higher mean captures of uninfected beetles ($F_{1,30} = 6.809$, $P = 0.014$). There was no evidence that bark beetle activity affected mean captures ($F_{1,30}=0.188$, $P=0.667$); nor was

there evidence of an interaction between PWN infection status and bark beetle activity ($F_{1,30}=0.323$, $P = 0.574$).

Inspection of residuals revealed a non-normal distribution (Shapiro–Wilk test; $P < 0.001$), so we also ran a generalized linear model (GLM) with a Poisson distribution. Results from the GLM were consistent with the ANOVA, showing a significant main effect of infection status ($\beta=-1.634$), confirming that more uninfected *M.scutellatus* were captured than PWN-positive beetles. However, with this model a significant effect of bark beetle activity on *M. scutellatus* abundance was also detected ($\beta=0.379$), suggesting that more *M. scutellatus* were trapped in stands that had experienced bark beetle mortality (Figure 2.3). The interaction between infection status and bark beetle presence was marginally significant ($\beta=-0.438$; Table 2.1), suggesting weak evidence that more uninfected beetles were trapped in bark-beetle affected stands than in non-affected stands.

No measured factors, including stand condition (% basal area mortality), proximity to spruce beetle-affected stands (m), nor beetle sex were associated with the probability of PWN infection in vectors (Table 2.2).

Mean *M. scutellatus* mass differed significantly due to the effects of stand condition ($\beta=-0.020$), with individuals collected inside spruce beetle-affected stands exhibiting 9.12% lower average mass than those from unaffected stands. No other measured factors including beetle sex, infection status, nor any interaction term affected mean beetle mass (Table 2.3, Figure 2.4).

Analysis of flight phenology via interpretation of cumulative trap capture curves for infected and uninfected beetles revealed similar patterns, with strongly overlapping 95%

confidence interval across the flight period (Figure 2.5). Estimated peak flight dates were day 202 for uninfected beetles and day 216 for infected beetles, differing by about 14 days. Despite this difference, the overlapping confidence intervals indicate no statistically distinct shift in flight timing between infection groups.

2.4 Discussion

This study demonstrates that while abiotically-driven forest disturbance (i.e., wildfire, Chapter 1) can influence vector-pathogen relationships, spruce beetle outbreak does not have similar effects on relationships between *Monochamus* beetles and pine wood nematode (*B. xylophilus*) in Colorado forests. Ecological disturbances are becoming more frequent and severe under ongoing climate change, increasing tree stress, with potential consequences for forest susceptibility to insects and pathogens (Ayres & Lombardero 2000). Fire and bark beetle outbreaks represent contrasting disturbance processes: fires release large amounts of energy in short pulses, consuming biomass and restructuring forests rapidly, while beetle outbreaks progress comparatively slowly (Seidl et al. 2017; Turner 2010). In addition, fires are generally more homogenous in their effects on trees than bark beetle outbreaks, which are patchily distributed and affect only trees of a specific size or age class (Seidle et al. 2017). These processes also differ by forest type. Ponderosa pine forests, studied in Chapter 1, occur at lower elevations with warmer and drier conditions and a history of frequent, low-severity fire that maintains disturbance-adapted stands (Fitzgerald 2005; McKinney 2019). In contrast, subalpine spruce–fir forests (present study) are cooler with more precipitation and experience infrequent, high-severity disturbances

(Schoennagel et al. 2004; Morris et al. 2015). These ecosystems are more stable between events and less physiologically adapted to recurrent stress. Because of these ecological and physiological contrasts, disturbance type and forest context likely determine outcomes for vector–pathogen relationships. Our findings suggest that prolonged biotic disturbances, such as spruce beetle outbreaks, do not restructure vector-pathogen relationships in the same way that acute, high-energy events like fire can.

Monochamus scutellatus abundance increased in stands with evidence of recent spruce beetle mortality, consistent with attraction to host volatiles released from stressed or dying wood, as well as bark beetle pheromones (Allison et al. 2001; Costello et al. 2011; Atkins et al. 2021). However, the probability that *M. scutellatus* was infected *B. xylophilus* did not differ between stands that were affected or unaffected by spruce beetle, suggesting that increased vector abundance did not translate to greater potential infection risk. The probability of infection is likely attributable to the lifecycle and host requirements of PWN itself. *Bursaphelenchus xylophilus* primarily infects pines, where it reproduces rapidly after resin flow ceases, and resin canals provide pathways for movement. Early larval stages feed on the parenchyma cells within these canals, while later stages shift to fungal feeding as tissues decay (Mamiya 1983). Pines possess large, abundant resin canals and parenchyma-rich xylem, whereas spruce and fir have smaller canals or lack axial parenchyma altogether (Wiedenhoeft 2010; Rosner & Hannrup 2004; Rodríguez-García et al. 2023). Moreover, pine secondary metabolites strongly promote nematode molting into dauerlarvae before they enter pupating *Monochamus*, while this molting process is much less efficient in non-pine tissues (Mamiya 1983). These host structural and chemical

differences, combined with nematode temperature requirements of 25 °C or over for disease persistence, are not suitable for persistence in high elevation spruce-fir forests. Cooler temperature drive latency in pine wilt disease progression; these factors likely prevent disease development despite the presence of infected vectors (Mamiya 1983).

Although more abundant, *M. scutellatus* collected from outbreak-affected spruce stands were smaller on average than those from healthy stands, suggesting that disturbance influenced some aspect of habitat quality or competitive pressures. This result was surprising due to reports of *Monochamus* predation on bark beetles (Schoeller et al. 2012). Since both species (*M. scutellatus* and *D. rufipennis*) occupy sapwood and consume phloem, scramble competition may occur when bark beetles colonize first and deplete these tissues (Ray et al. 2019). Drought or biotic stress can also thin phloem and limit nutrient transport, effectively reducing host tissue quality for developing larvae (Christiansen et al. 1987; Bentz et al. 2010; Fettig et al. 2022). Chronic stress of this type gradually erodes resource quality and can limit beetle growth and fitness (Anderegg et al. 2015). The patchy, asynchronous nature of spruce beetle outbreaks may compound these effects by creating unevenly aged resource patches across the landscape.

Infection status was not associated with clear shifts in flight phenology, and infected beetles flew slightly later than uninfected individuals—opposite to the post-fire pattern observed in Chapter 1. This may be due to differences in disturbance age or intensity. Wildfire is a comparatively short-lived event that creates a clear, synchronous pulse of host stress, while bark beetle outbreaks progress over multiple years, producing overlapping patches of mortality and a diffuse “disturbance age” mosaic (Seidl et al. 2017).

Without a well-defined post-disturbance window of susceptibility, there is little ecological pressure for infected vectors to emerge earlier or change their behavior as is reported in other systems (Cator et al. 2012; Carmo-Sousa et al. 2014, Chapter 1). The observed differences in patterns of infected vector flight phenology between the two studies (Chapter 1 and the present study) may also reflect differences in the forest types studied here: since Engelmann spruce is not generally a host for *B. xylophilus* it could be the case that infected *M. scutellatus* are recruiting to baited pheromone traps from locations that were distal to the study site (e.g., from proximal lodgepole pine stands).

In addition, some methodological limitations could have skewed our ability to compare phenological patterns between the two study systems. Our flight phenology curves (Figure 4.4) indicate that trapping was initiated partway through the flight season; thus, it is possible that even if a pattern of earlier flight by infected *M. scutellatus* occurred, we would not have been able to detect this. To our knowledge this is the first study to report on the flight phenology of *M. scutellatus* in high elevation spruce-fir forests in the southern Rocky Mountains, and flight appears to occur earlier and more synchronously than is found in lower-elevation ponderosa pine forests (Atkins et al. 2021). Future studies could improve flight phenology estimates in this system by extending trapping from early June through September to capture the complete flight period of *M. scutellatus* at high elevations.

Comparing the collective results of both studies (Chapter 1 and Chapter 2), I conclude that post-disturbance vector-pathogen relationships depend on disturbance type (biotic vs. abiotic), time-since-disturbance, vector species (*M. scutellatus* vs. *M. clamator*), and forest type (spruce vs. pine forest). Monitoring and disease management efforts should

therefore prioritize recently burned sites over those affected by bark beetle outbreak, which does not appear to affect the occurrence of *B. xylophilus* in *M. scutellatus* despite being associated with increased vector abundance. The influence of bark beetle outbreaks on *B. xylophilus* – *Monochamus* relationships in other systems, such lodgepole and ponderosa pine forests, nonetheless merits further investigation as vector-pathogen relationships may respond differently in ecosystems where pines are the dominant forest tree.

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Table 2.1 A summary of a generalized linear model analyzing the effects of *M. scutellatus* infection status, bark beetle activity, and their interaction on the mean abundance of *M. scutellatus* trap captures.

Parameter	Estimate	SE	Z-value	P-value
Intercept	3.209	0.066	47.935	<0.001
Bark beetle activity	0.379	0.085	4.453	<0.001
Infection status	-1.634	0.197	-8,280	<0.001
Activity * infection status	-0.438	0.257	-1.705	0.088

Table 2.2 Summary of a binomial GLM testing effects of basal area mortality (%), distance to spruce beetle kill (m), and beetle sex (male or female) on the probability of PWN infection in *M. scutellatus*.

Parameter	Estimate (β)	SE	Z-value	P
Intercept	-2.429	0.380	-6.388	< 0.0001
Basal area dead (%)	0.004	0.006	0.668	0.504
Distance (m)	0.000	0.000	1.240	0.215
Sex (male)	-0.014	0.255	-0.056	0.955

Table 2.3 Summary of a generalized linear model analyzing the effects of beetle sex, infection status, spruce beetle activity (stand condition), and all two- and three-way interactions on the mass (mg) of *M. scutellatus* captured in this study.

Parameter	Estimate (β)	SE	Z-value	P
Intercept	0.178	0.007	24.032	<0.001
Sex (male)	-0.016	0.010	-1.557	0.120
Infection status (infected)	-0.012	0.024	-0.483	0.630
Stand condition (affected)	-0.021	0.010	-2.130	0.034
Sex x infection	-0.027	0.031	-0.887	0.375
Sex x Stand condition	0.006	0.013	0.460	0.646
Infection x Stand condition	0.035	0.030	1.160	0.246
Sex x Infection x Stand condition	-0.032	0.040	-0.793	0.428

Spruce Beetle Disturbance and Study Sites in Colorado

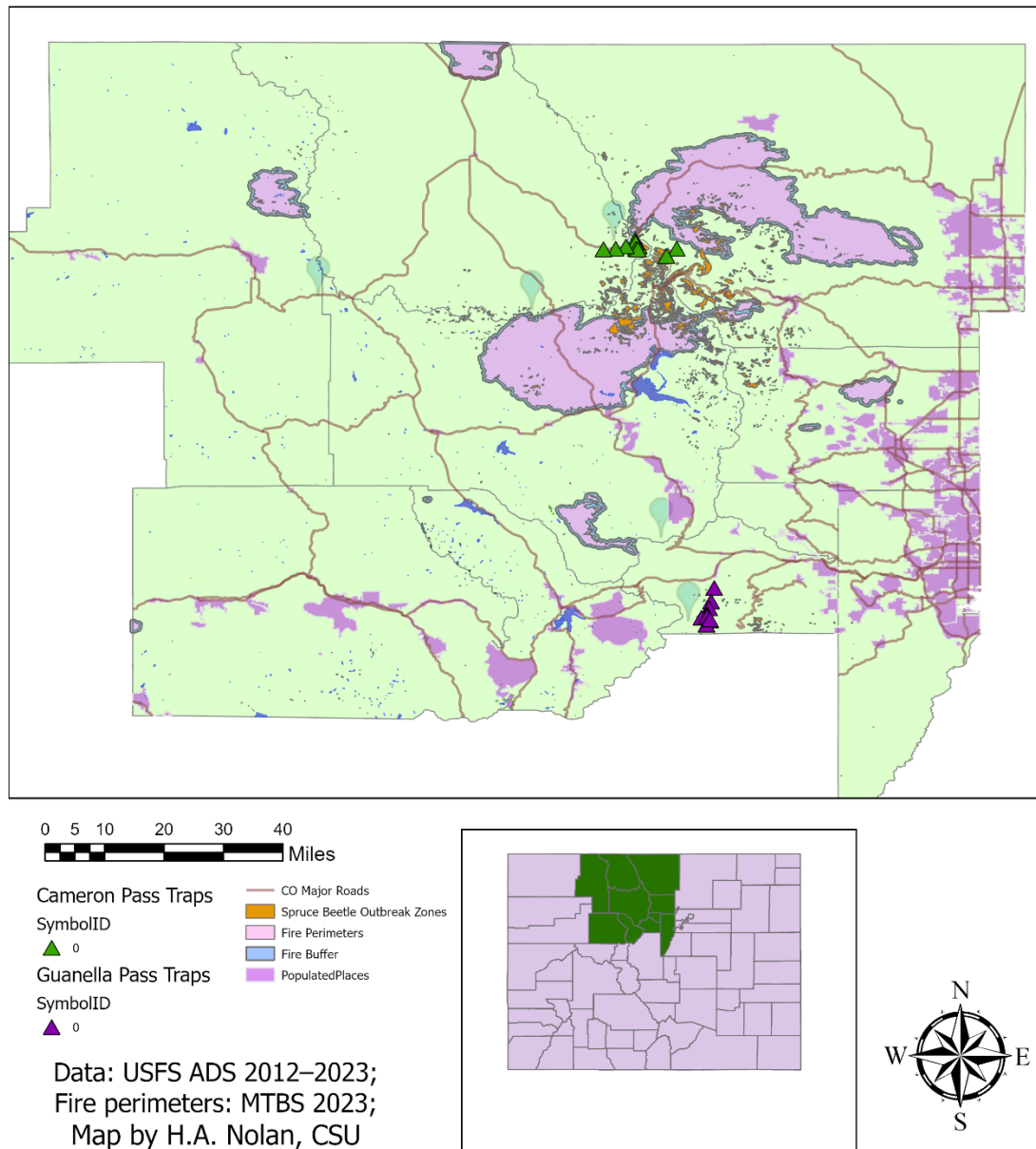


Figure 2.1 Map of study sites and trap locations in Larimer, Jackson, and Clear Creek counties, spruce beetle polygons, burn perimeters, and their boundaries.

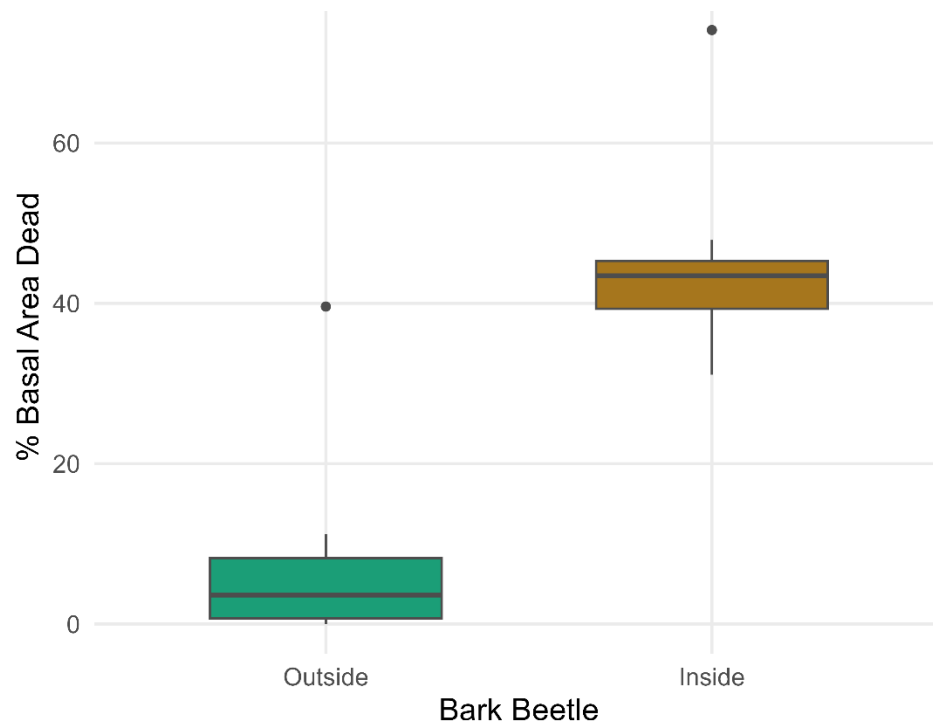


Figure 2.2 A box-and-whiskers plot showing the distributions of the proportion of dead basal area (%) in stands affected by ('inside') and unaffected ('outside') by spruce beetle. Median basal area mortality was notably higher in stands affected by spruce beetle.

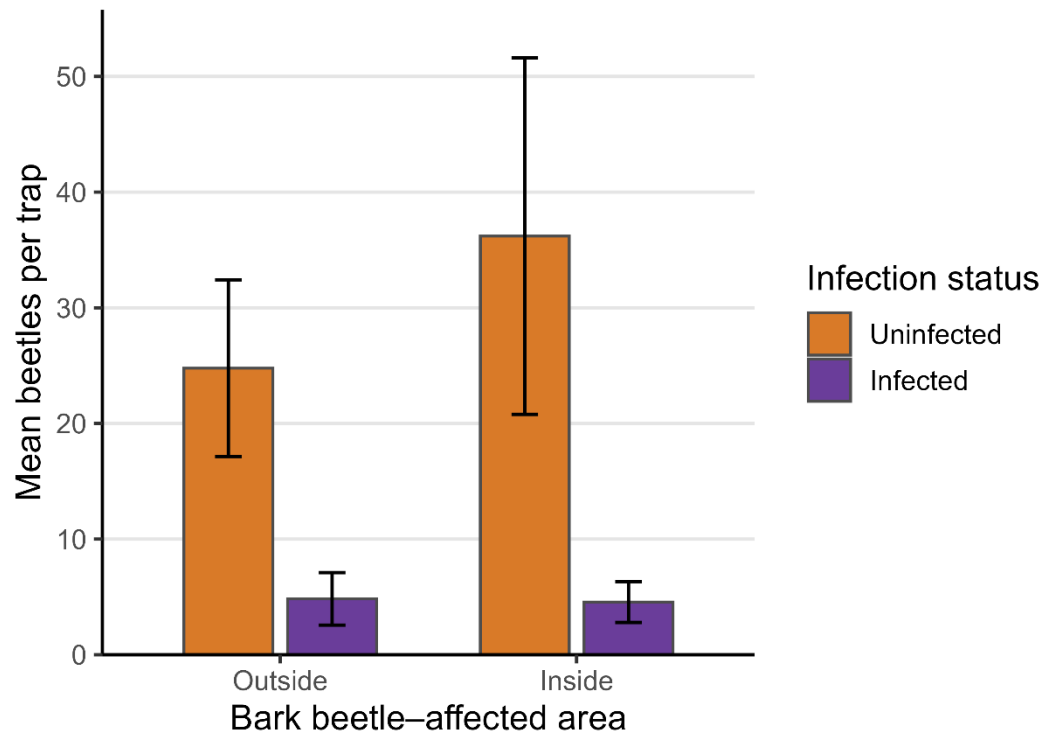


Figure 2.3 Variation in mean trap captures of *M. scutellatus*, relative to beetle PWN infection status, between spruce beetle affected ('inside') and unaffected ('outside') stands. Bars represent plus or minus one standard error of the mean.

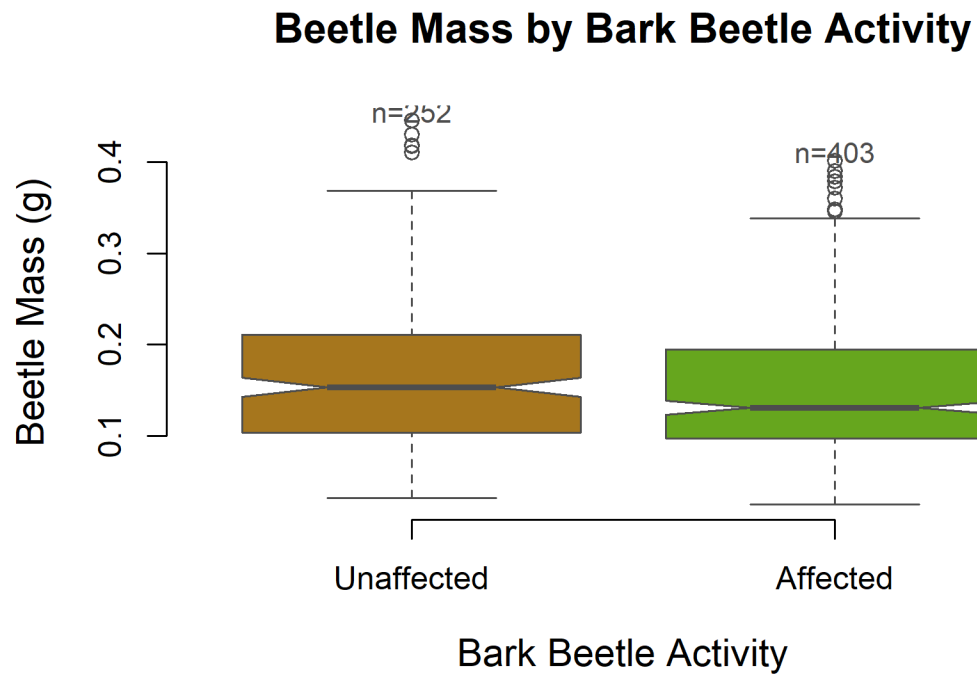


Figure 2.4 Boxplot comparing beetle mass of *M. scutellatus* in spruce beetle-affected ('inside') and unaffected ('outside') stands.

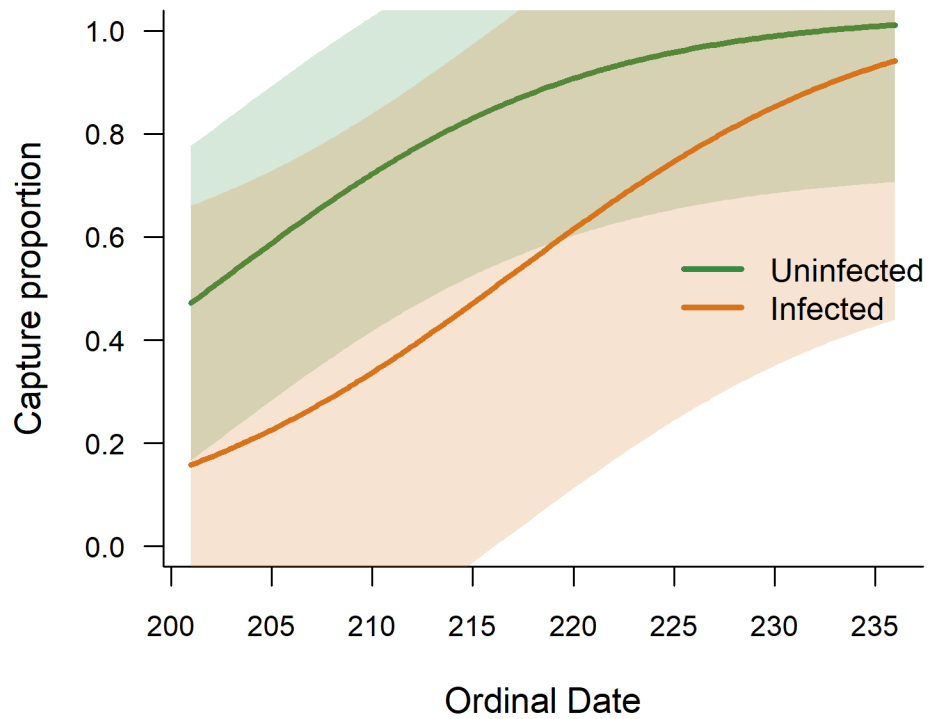


Figure 2.5 Cumulative capture flight curves of *M.scutellatus* over trapping period (Ordinal Date). Orange represents uninfected and green represents infected *M.scutellatus*.