

**Playing with fire: *Dendroctonus ponderosae* (mountain pine beetles) in post-burn lodgepole pine forests**

by

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## Abstract

*Dendroctonus ponderosae*, an aggressive tree-killing bark beetle, is one of the most significant insects in the coniferous forests of western North America. Although *D. ponderosae* is restricted to weakened host trees at low-density populations, fire can suddenly increase the number of suitable, less-defended hosts, and potentially allow increased beetle colonisation and population growth. However, it is unclear whether *D. ponderosae* is attracted to fire-injured hosts or whether post-burn forest stands can promote outbreaks. In this thesis, I address this and several related questions by examining *D. ponderosae* interactions with both fire and the broader subcortical insect community at three sites in the Rocky Mountains of Alberta, Canada. I showed that proportionally more fire-injured trees were attacked than non-burned trees every year for 4 years after fire, and that beetle density per tree was always greater on fire-injured trees. Next, I showed that prescribed fire likely does not promote outbreaks of *D. ponderosae*: at one of three sites, colonisation declined after an initial response to a resource pulse, and at the remaining two sites, colonisation remained low over time. Additionally, neither the proportion of trees attacked nor the number of attacks per tree increased in adjacent non-burned stands, which would have indicated local population increase associated with the impact of fire. However, I observed stabilisation of *D. ponderosae* colonisation 4 years after fire at one site, and ongoing low rates of attack at the remaining sites, potentially indicating that fires serve as refugia for low-density populations of *D. ponderosae*. Various factors appear to negatively impact *D. ponderosae*, interfering with its ability to take advantage of post-fire stands. First, although declining resource (phloem) quality likely does not explain why *D. ponderosae* cannot take advantage of a post-fire stand, I show that declining resource quantity, i.e., preferred trees dying

soon after fire, probably affects the beetles negatively in their host-searching phase 1 year after fire. Second, fire-injured trees attract a diverse subcortical insect community, including competitors and predators of *D. ponderosae*. I show that this community, especially other bark beetles that compete directly with *D. ponderosae*, is associated with areas containing *D. ponderosae*. Thus, post-fire forest stands likely intensify interspecific interactions for *D. ponderosae*, especially competition. To test these interactions, I used passive traps to examine the subcortical communities present in burned and adjacent non-burned stands because using lures would have artificially aggregated insects and mixed samples. I compared trap efficiencies and found that landing traps, placed directly on host trees, catch more individuals per unit area than flight intercept traps. However, intercept traps catch a greater number of species, especially Hymenoptera. Overall, I show that although low-density populations of *D. ponderosae* can use post-fire stands as refugia from extirpation until new weakened host trees arise on the landscape, various factors interact to suppress potential population growth and outbreak.

## **Preface**

Chapter 3 of this thesis is part of a collaboration with Dr. Nadir Erbilgin at the University of Alberta and has been published as: Tabacaru, C.A., Erbilgin, N., 2015. Competitors and natural enemies may cumulatively mediate *Dendroctonus ponderosae* colonization of burned *Pinus* forests. *Forest Ecology and Management* 337: 98–109. I performed the data collection and analysis and composed the manuscript. N. Erbilgin was the supervisory author and was involved with concept formation and manuscript composition.

*To my grandparents.*

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# Chapter 1

## Introduction

### 1.1 Fire and insects as disturbances

In forested ecosystems, disturbances and their interactions shape structure and biodiversity, creating species and microclimate mosaics (Bigler et al. 2005). Two such disturbance agents, fire and insects, are major components of most forests and their interactions affect nutrient cycling and species composition (see review by McCullough et al. 1998 and Kurz et al. 2008). Further, interactions among biotic agents may be mediated by abiotic disturbances such as fire (e.g., Elderd 2006).

Fire influences nutrient cycles, regeneration, and productivity of forests, mainly by affecting soil (e.g., Bonan and Shugart 1989). Infrequent, stand-replacing fires have shaped the distribution and composition of seral pine stands (e.g., Arno 1980; Romme and Knight 1982; Sibold et al. 2006). *Pinus contorta* (lodgepole pine), for example, has evolved with fire to ensure reproductive success; fire is required to open its generally serotinous cones (Amman and Schmitz 1988). Forest fire interacts with other major disturbance agents, such as insects, to determine the ultimate nature of the landscape (Jenkins et al. 2008).

Anthropogenic factors such as forest management practices (e.g., fire suppression) have increased the size and intensity of insect epidemics in North America over the last century (e.g., Haack and Byler 1993; Parker et al. 2006). Consequently, insect and pathogen outbreaks in the U.S.A. cause more forest disturbances than any other factor, including fire (e.g., Haack and Byler 1993). Subcortical insects such as bark beetles and wood borers can directly control succession for many tree species (Franklin et al. 1987) by preferentially attacking old or weakened trees, thereby opening forest gaps and contributing to a heterogeneous landscape, which increases stand fitness (Burdon 1991; Axelson et al. 2009). Some tend to slow succession; for example, *Dendroctonus ponderosae* Hopkins (mountain pine beetle) kills old *P. contorta* in the absence of fire (Haack and Byler 1993). However, fires provide weakened trees for subcortical insects and pathogens (e.g., Six and Skov 2009), and so may interact with insect disturbance agents to produce indirect and unpredictable changes in a forest ecosystem.

## **1.2 The *Dendroctonus ponderosae*-*Pinus contorta* system**

*Dendroctonus ponderosae*, an aggressive tree-killing bark beetle (termed primary), is the most significant insect in *P. contorta* forests in western North America (Amman and Baker 1972; Li et al. 2005; Bentz et al. 2010). Attacks are initiated by females, which then produce an aggregating pheromone (Pitman and Vité 1969); along with volatile terpenes from the tree, this attracts additional beetles, potentially translating into a mass attack that can overwhelm even the healthiest, most resistant trees (Amman and Schmitz 1988). Post-attack tree death is thought to result from a combination of larval tunnelling as they feed on phloem at right angles to egg galleries, which girdles the tree, and blue-stain fungi (*Ophiostoma montium* and *Grosmannia clavigera*) carried

by the adult beetles (Amman and Schmitz 1988). The latter may assist *D. ponderosae* in overcoming secondary host defences by impeding conduction (Raffa and Berryman 1983; Amman and Schmitz 1988). *Dendroctonus ponderosae* is generally univoltine (one generation per year), but can be semivoltine (one generation every two years) at higher elevations (Reid 1962; Bentz et al. 2014). Population dynamics of primary bark beetles such as *D. ponderosae* are characterised by long periods at low-density populations, during which the beetles only attack weakened trees, interspersed by outbreaks during which healthy trees are attacked and killed. Outbreaks occur after an “incipient-epidemic” stage, during which the population has risen enough to successfully attack average large diameter trees, which would be too well-defended to be attacked by a low-density population. (Carroll et al. 2006). If conditions remain conducive to population increase, the incipient-epidemic stage gives way to the outbreak stage, when beetles increase at a high rate and spread across the landscape. Historically, *D. ponderosae* outbreaks have occurred throughout North America’s *P. contorta* forests, causing periodic large-scale disturbances (Robertson et al. 2009). Some factors thought to have a role in regulating populations and thus in inducing outbreaks are the availability of suitable hosts, stand conditions, environmental factors, and the abundance of parasites and predators (Jenkins et al. 2008). As a natural and endemic disturbance agent, *D. ponderosae* is deeply integrated into the historical disturbance regime of western Canadian forests and is an essential part of maintaining healthy forest ecosystems (Parker et al. 2006; Kurz et al. 2008).

### **1.3 Fire and *Dendroctonus ponderosae***

Fire and *D. ponderosae* have a complex relationship and affect each other in multiple ways. For example, the beetles cause extensive and relatively rapid *P. contorta* mor-

tality, thus increasing fuel loads and, in turn, the potential for fire (e.g., Jenkins et al. 2008, but see Page et al. 2014 for a critical review of predictive fire models). Conversely, *D. ponderosae* may prefer to attack fire-injured trees (Stock and Gorley 1989). Physiologically, stressed trees may be more susceptible to attack by *D. ponderosae* (Waring and Pitman 1983) and fire poses the risk of leaving live, yet partially burned—and therefore stressed—trees in its wake. Such trees may attract the beetles (Thomas and Agee 1986; McCullough et al. 1998; Jenkins et al. 2008; Powell et al. 2012) as they may lower the critical minimum number of individuals required to overcome host defences (Fettig et al. 2007). This may subsequently promote *D. ponderosae* population growth in burned areas and allow the beetles to overwhelm otherwise healthy adjacent trees. However, contradictory results at the tree level have shown that *D. ponderosae* does not prefer burned trees but is more likely to succeed in overwhelming them once attacked (Elkin and Reid 2004).

Management strategies in Alberta have used fire both directly and indirectly as a tool to control *D. ponderosae* populations. Direct uses include burning felled or standing individual trees or burning whole stands after pheromone baits congregate beetles into a small area (Trzcinski and Reid 2008), two of the earliest methods of control (Safranyik et al. 2001). Indirectly, and more recently, fire has been used to remove potential host trees before attack (Whitehead et al. 2006). Alberta Environment and Sustainable Resource Development is currently implementing the Pine Strategy (ASRD 2007) which aims to reduce the area of *D. ponderosae*-susceptible stands by 75% over the next 20 years. This plan, while utilising logging and other harvesting methods, must also incorporate fire where harvesting is not possible, such as in protected areas and parks. However, the success of these tactics depends on how the beetles respond to fire-damaged trees (Elkin and Reid 2004).

*Dendroctonus ponderosae* responses to fire are most likely mediated by community interactions, which have not been extensively studied post-fire. The beetles have evolved with a multitude of generalist and specialist natural enemies and competitors that affect their populations at endemic levels (Boone et al. 2008). Predatory beetles and flies (Boone et al. 2008), insect competitors (Boone et al. 2008), and various parasites (Steiner 1932) and parasitoids (DeLeon 1934) are just some of the organisms that negatively interact with *D. ponderosae*. Some of these are known to be attracted to fire-injured trees; for example, *Ips pini*, a competitor, is positively affected by fire (Six and Skov 2009). Thus, it is probable that collectively, the subcortical community influences *D. ponderosae* responses.

## 1.4 The chapters ahead

In this thesis, I aim to describe the events following prescribed fire with respect to *D. ponderosae* and its associated subcortical insect community. In Chapter 2, given that fire injury stresses trees, which can increase their susceptibility to *D. ponderosae* attack (Waring and Pitman 1983), I test the unresolved hypothesis that endemic *D. ponderosae* preferentially attacks burned trees. I further test if post-fire stands can promote bark beetle outbreaks or suppress their populations. Lastly, I assess potential mechanisms driving post-fire patterns by testing whether resource quality (i.e., phloem quality) or quantity (i.e., number of susceptible hosts) changes over time. In Chapter 2, I show that although *D. ponderosae* responded to a resource pulse 1 year after fire, attacks then declined over the next 3 years. Thus, in Chapter 3, I survey the subcortical community after fire to address a potential mechanism explaining why *D. ponderosae* was unable to increase its population after fire: increased interspecies interactions. Results pointed to increased interactions, specifically with direct competitors, i.e., other bark

beetles. Chapter 4 therefore addresses the specific responses of the bark and ambrosia beetle community to fire, and how these responses can affect *D. ponderosae*. Finally, in Chapter 5, I necessarily digress from the linear story of the previous chapters to provide an important detailed comparison of the passive insect trap types I used during my work. This comparison may be vital for researchers aiming to survey insects without attracting them with baits. Overall, my thesis characterises the effects of prescribed fire in *P. contorta* forests from the point of view of a tree-killing bark beetle and the subcortical community as a whole, while providing logistical recommendations for subcortical insect research.

## **Chapter 2**

# **Prescribed fire does not promote outbreaks of a primary bark beetle at low-density populations**

### **2.1 Introduction**

Bark beetles (Coleoptera: Curculionidae: Scolytinae) provide important ecological functions in forest ecosystems, affecting species composition and canopy thinning (Kurz et al. 2008; Bentz et al. 2010). Populations of some bark beetle species, termed primary or tree-killing because they can attack and kill live trees, undergo periodic fluctuations in abundance (Bentz et al. 2010). They remain at low levels for decades, suppressed by natural enemies and losses incurred during dispersal, and are restricted to hosts with weakened defences (Raffa and Berryman 1980), which are typically rare across the landscape. However, they can rise and enter an outbreak phase, in which host mortality is high, potentially over millions of hectares (Raffa et al. 2008; Bentz et al. 2010; Safranyik et al. 2010). At outbreak levels, bark beetles influence forest structure and



species composition, and can alter forest succession (Bentz et al. 2010). However, the underlying dynamics that shift a population to outbreak levels are poorly understood.

Host tree condition and abundance, and more recently climate warming, are important drivers of bark beetle outbreaks (Raffa and Berryman 1980; Økland and Berryman 2004; Bentz et al. 2010). A shift in host condition can occur either slowly or suddenly. Longer-term stresses, such as drought, can alter host susceptibility, but may also impact beetles by altering the quantity and quality of host phloem, their main food source (Jactel et al. 2012). Conversely, events such as fire can suddenly alter host susceptibility, e.g., by lowering defences of even the largest trees (Powell and Raffa 2011), in which beetle reproduction is highest (Amman 1972). Fire may therefore promote beetle colonisation and population growth by suddenly increasing the number of suitable, less-defended hosts (Berryman 1976; Amman and Ryan 1991; Powell et al. 2012; Stark et al. 2013). However, results with primary bark beetles are contradictory, even within species. For example, Elkin and Reid (2004) found no difference in *Dendroctonus ponderosae* Hopkins (mountain pine beetle) attacks between burned and non-burned trees, but Powell et al. (2012) found increased colonisation of burned trees.

Fire itself can influence forest ecosystem functions by altering key processes like nutrient cycling, regeneration, and productivity—all important in maintaining forest resiliency (Folke et al. 2004). Fire suppression over the last century has increased forest susceptibility to insect outbreaks in many North American forests (Parker et al. 2006). This suggests a close relationship between fire, fire-dependent forest ecosystems, and insect outbreaks (Mattson and Addy 1975; Jenkins et al. 2008). As an important management tool for North American forests, prescribed fire has recently been used to restore vegetation types and improve forest heterogeneity (White et al. 2011; Ryan et al. 2013). Thus, understanding its long-term effects in areas with low-density

populations of primary bark beetles is critical to assessing the full impact of fire on ecosystems (Fettig et al. 2008).

Two competing hypotheses have been proposed to explain how fire affects low-density populations of primary bark beetles, assuming that fire-injured trees are preferentially attacked: 1) fires trigger population growth, shifting a population to outbreak levels (Rasmussen et al. 1996; McHugh et al. 2003), or 2) fires initially cause beetles to congregate, but subsequently create an environment in which initially high populations decline (Miller and Patterson 1927; Powell et al. 2012). Past studies have generally monitored bark beetle attacks for just 1 year after fire (e.g., Elkin and Reid 2004; Powell et al. 2012), which may provide an incomplete picture and potentially explain the array of contradictory predictions. While these studies have provided valuable insights, there is a clear need for longer-term research in understanding the complex role of fire in the population dynamics of primary bark beetles.

To address this need, I monitored *D. ponderosae* attacks at low-density population levels in *Pinus contorta* var. *latifolia* (lodgepole pine) forests for 4 years after fire. *Dendroctonus ponderosae* is the most important biotic forest disturbance agent in western North America and a prototypical example of a primary bark beetle that is restricted to stressed hosts at low population levels (Safranyik et al. 2010), but undergoes periodic outbreaks (Raffa et al. 2008). The beetles spend almost their entire life cycle in the phloem of *P. contorta* (Safranyik et al. 2010); thus, changes in the quality and quantity of phloem can impact all *D. ponderosae* life stages. Fire is used to manage *P. contorta* forests with various goals, including the reduction of host availability for *D. ponderosae*.

With this in mind, our study encompasses three interconnected objectives, carried out in the *P. contorta* forests of Alberta, Canada. First, given that fire injury stresses trees, which can increase their susceptibility to *D. ponderosae* attack (Waring and Pit-

man 1983), I tested the unresolved hypothesis that *D. ponderosae* at low-density population levels preferentially attack burned trees. Second, if this hypothesis was supported, I sought to test the competing hypotheses that post-fire stands can either promote bark beetle outbreaks, a scenario in which I would expect to see increased attacks in adjacent non-burned stands over time, or provide only short-term resource pulses, after which populations decline over time. Third, if results showed that post-fire stands do not promote *D. ponderosae* outbreaks, I further sought to assess potential mechanisms driving this phenomenon by testing whether resource quality (i.e., phloem quality) or quantity (i.e., number of susceptible hosts) declines. Overall, this study offers a unique, long-term perspective on several unresolved and topical questions relevant to both ecologists and land managers.

## **2.2 Materials and methods**

### **2.2.1 Assessing *Dendroctonus ponderosae* attacks on burned and non-burned *Pinus contorta***

Research occurred in three mature *P. contorta* forests within the Alberta Rocky Mountains, burned as part of prescribed fire programs in spring 2009. The Mt. Nestor fire (115° 22'55.617" W, 50° 54'25.073" N; elevation of centre 1800 m) encompassed 618 ha, was undertaken primarily to improve habitat for grizzly bears (*Ursus arctos*), bighorn sheep (*Ovis canadensis*), and whitebark pine (*Pinus albicaulis*), and mainly occurred in stands with a 200–250 year fire cycle (Rogean et al. 2004). The Upper Saskatchewan fire (116° 37'2.310" W, 52° 1'17.964" N; elevation of centre 1400 m) encompassed 4,623 ha and was undertaken to reduce the amount of *P. contorta* susceptible to *D. ponderosae* and to restore natural fire regime vegetation types. The majority occurred in areas with a 100–150 year fire cycle, with small portions in upper

elevations with 201–250 and 251–300 year fire cycles (Rogeanu et al. 2004). The Ya Ha Tinda fire (115° 36'35.079" W, 51° 44'07.784" N; elevation of centre 1700 m) encompassed 1,264 ha, was undertaken primarily to reduce the amount of *P. contorta* susceptible to *D. ponderosae*, and occurred in areas with a 64–98 year fire cycle (Rogeanu 2009). The severity of fire injury to trees was variable in all burns, and some areas experienced stand-replacing fire. All forests contained low-density populations of *D. ponderosae* and were separated by > 100 km. In this part of the Rocky Mountains, low to medium intensity fires are common, but large, stand-replacing fires also occur (Arno 1980).

I assessed how fire injury affects *D. ponderosae* attack at both plot and tree levels for 4 years. I used Parks Canada burn severity classifications, determined using US Geological Survey techniques (Soverel et al. 2010), to define three fire injury classes: non-burned, low, and moderate. I used ArcGIS 9.2 (ESRI, Redlands, CA, U.S.A.) to locate at least 15 10 × 10 m plots, a minimum of 200 m apart to avoid clumping, throughout each fire injury class at each site. I ground-truthed Parks Canada's classifications as fire injuries on the ground may vary on a finer scale than is discernible from the air. After plot establishment, I estimated average bole char (the percentage of each trunk that was charred) per plot (average of all individual tree values, estimated ocularly) as a general measure of fire injury. Parks Canada's non-burned, low, and moderate classes corresponded to 0% bole char, 1%–15% (mean for all sites 10.86%) bole char, and ≥ 16% (mean 31.42%) bole char, respectively. Occasionally, ground-truthing necessitated placing a moderate plot in a low area or vice-versa. I placed non-burned plots within 2 km of burns to ensure that beetles could reach them within a flight season (Safranyik and Carroll 2006). Within each plot, I tagged *P. contorta* trees > 15 cm in diameter at breast height (DBH; 1.3 m from the forest floor), and measured diameter and phloem thickness at breast height. Phloem was collected in 1 × 1-cm samples us-

Table 2.1: Summaries of plots, trees, DBH, bole char, duff char, and bole char height for three sites (Mt. Nestor, Upper Saskatchewan, and the Ya Ha Tinda Ranch), divided among fire injury classes. Information regarding classes is provided in materials and methods. All means are  $\pm$  SE, where SE was determined using the number of plots as sample size. n/a = not applicable.

	Nr. Plots	Nr. Trees	Mean DBH (cm)	Mean bole char (%)	Mean duff char (%)	Mean bole char height (m)
<b>Mt. Nestor</b>						
Non-burned	15	158	22.96 $\pm$ 1.52	n/a	n/a	n/a
Low	16	162	25.03 $\pm$ 1.53	8.65 $\pm$ 1.04	80.62 $\pm$ 4.35	1.28 $\pm$ 0.17
Moderate	14	107	25.17 $\pm$ 1.69	28.89 $\pm$ 2.17	94.21 $\pm$ 2.33	3.55 $\pm$ 0.23
<b>Upper Saskatchewan</b>						
Non-burned	16	175	24.12 $\pm$ 1.55	n/a	n/a	n/a
Low	19	210	22.32 $\pm$ 1.16	8.19 $\pm$ 0.99	81.91 $\pm$ 4.07	1.48 $\pm$ 0.20
Moderate	15	96	23.03 $\pm$ 1.30	36.14 $\pm$ 5.12	97.66 $\pm$ 1.01	6.42 $\pm$ 1.03
<b>Ya Ha Tinda</b>						
Non-burned	15	134	27.76 $\pm$ 1.72	n/a	n/a	n/a
Low	7	63	23.78 $\pm$ 1.85	11.33 $\pm$ 1.13	81.53 $\pm$ 6.22	2.31 $\pm$ 0.30
Moderate	23	180	26.02 $\pm$ 0.95	29.22 $\pm$ 1.95	95.90 $\pm$ 1.32	5.21 $\pm$ 0.29

ing a chisel, at the north and south sides of each tree, and its thickness was measured using callipers. To measure tree fire injury, I estimated bole char, bole char height (the maximum height of the charred area on each trunk), and duff char (the percentage of the forest floor organic layer that was burned in a 1-m-diameter circle around the base of each tree).

To determine beetle activity, I quantified attacks in each plot for 4 consecutive years (2009–2012). Attacks were determined by the presence of yellow pitch tubes (exuded sap), characteristic of *D. ponderosae*, and boring dust, counted above 1 m on the trunk to avoid lower-stem secondary bark beetles. If I was unsure of an attack, I removed the bark and observed *D. ponderosae* tunnels. I did not attempt to determine specific causes of tree mortality, but trees were generally killed by factors others than *D. ponderosae*. Tree death was observed from 2010 to 2012, and reflected mortality from the previous fall to the current summer (e.g., 2010 mortality reflects tree death between fall 2009 and summer 2010). Overall, I monitored 1,285 trees in 140 sampling plots over a 4 year post-fire period (Table 2.1).

### 2.2.2 Phloem quality

I measured phloem nitrogen (N) and moisture in fire-injured trees to assess resource quality due to their importance to bark beetle reproduction and survival (Redmer et al. 2001; Goodsman et al. 2012). Since sampling phloem could damage trees and potentially affect beetle attack, I collected samples in August 2012, after all other data. I collected 1-year-post-fire phloem samples from the nearby Evan-Thomas prescribed burn in Kananaskis, Alberta (115° 6' 6.119" W, 50° 52' 31.508" N), burned in 2011 (n: non-burned = 33; low = 29; moderate = 22). I collected 3-year-post-fire phloem samples from the Mt. Nestor burn (n: non-burned = 27; low = 39; moderate = 24). Few prescribed fires were initiated in Alberta in 2010, so I was unable to locate an appropriate burn for 2-year-post-fire phloem samples. Trees > 15 cm in DBH were chosen randomly (no plots were placed) within the fire injury classes and two phloem samples (2 × 2 cm) were removed at breast height, at the north and south sides of each tree, and frozen. Where the north or south side was burned, I sampled the closest non-burned point because *D. ponderosae* does not attack charred phloem (Elkin and Reid 2004). Each sample was cut in half and the first halves of each tree's north and south samples were combined, ground in liquid nitrogen, dried overnight, and analysed for total N concentration by the Dumas Combustion Method using a Costech 4010 Elemental Analyzer System (Costech Analytical Technologies Inc., Valencia, CA, U.S.A.). The remaining halves were weighed, dried at 60°C in a drying oven for 72 h, and reweighed to determine moisture content (percent moisture of dry weight).

### 2.2.3 Statistical analyses

I used R 3.0.2 (R Development Core Team 2013) for all statistical analyses. For plot-level analyses, in addition to numbers of attacks per tree, I also focussed on the primary attraction of beetles to hosts, compared to the secondary attraction of beetles to con-

specifics (Safranyik et al. 2010); thus, I used both mean number of attacks per tree per plot and the proportion of trees attacked per plot. Each year, only live trees were assessed, so the number of trees available for beetle attack decreased with tree death. I performed separate analyses at each site because varying environmental variables can strongly affect beetle populations (e.g., Safranyik and Carroll 2006). Since our data could not meet the assumption of homogeneous variances, I used the Brunner-Dette-Munk test (*asbio* package in R) to determine differences in beetle attacks per tree and in the proportion of trees attacked among fire injury classes and years. This is a rank-based permutational ANOVA which does not assume normality or homogeneity of variances (Brunner et al. 1997). In addition, I used non-parametric multiple pairwise comparisons (Kruskal-Wallis comparisons; *asbio* package in R) to test differences in proportions of trees attacked among injury classes and years. I repeated the above analyses to determine differences in rates of tree death among injury classes and years at each site.

For tree-level analyses, I used data from all sites combined to gain an understanding of the general phenomena. I constructed three generalised linear mixed-effects models with logit transformations to test the importance of bole char (range 0%–90%), bole char height (0–25 m), and duff char (0%–100%), for beetle presence each year after fire. Sample sizes declined with year due to tree death from fire injury. I used mixed-effects models to account for any variation the experimental design (i.e., plot and site) imparted to the analysis at the tree level, with DBH as a covariate. I used likelihood ratio tests on nested models, where main effects were included or excluded, for model selection. Models were used to test the effects of fire injury on beetle attack, not to predict attack outside the sample.

To determine differences in total N concentration and percent moisture content of phloem among fire injury classes, I used linear mixed-effects models (*nlme* package in

R) with plot as a random effect and phloem thickness as a covariate. For all significant models, I used Tukey's multiple comparison method (*multcomp* package in R) to test differences among fire injury classes. Additionally, since *D. ponderosae* reproduction is affected by phloem thickness and beetles tend to attack larger trees (Amman 1972), I used Kruskal-Wallis tests to determine differences in phloem thickness among injury classes.

## 2.3 Results

### 2.3.1 *Dendroctonus ponderosae* attacks

At Mt. Nestor, the proportion of trees attacked and the number of attacks per tree (non-cumulative) differed among years (proportion:  $F_{2,36, 96.18} = 8.97, P < 0.001$ ; attacks:  $F_{2,40, 102.87} = 10.65, P < 0.001$ ; Fig. 2.1): 2009 had proportionally fewer attacked trees and fewer attacks per tree than both 2011 (proportion:  $P < 0.05$ ; attacks:  $P < 0.01$ ) and 2012 (proportion:  $P < 0.01$ ; attacks:  $P < 0.01$ ). However, because I found significant interactions among fire injury class and year for both the proportion of trees attacked ( $F_{4,34, 96.18} = 3.14, P < 0.05$ ; Fig. 2.1a) and the number of attacks per tree ( $F_{4,48, 102.87} = 3.89, P < 0.01$ ; Fig. 2.1b), I looked at the main effect of fire injury class for each year separately. The proportion of trees attacked differed among fire injury classes every year (Kruskal-Wallis test; 2009:  $\chi^2 = 25.16, df = 2, P < 0.001$ ; 2010:  $\chi^2 = 25.80, df = 2, P < 0.001$ ; 2011:  $\chi^2 = 7.48, df = 2, P < 0.05$ ; 2012:  $\chi^2 = 9.63, df = 2, P < 0.01$ ). Specifically, in 2009, moderate plots had proportionally more attacked trees than low ( $P < 0.01$ ) and non-burned ( $P < 0.001$ ) plots. In 2010, again moderate plots had proportionally more attacked trees than low ( $P < 0.001$ ) and non-burned ( $P < 0.001$ ) plots. In 2011, moderate plots had proportionally more attacked trees than non-burned plots ( $P < 0.05$ ). Finally, in 2012, moderate plots had proportionally more



attacked trees than non-burned plots ( $P < 0.05$ ). Similarly, the number of attacks per tree differed among fire injury classes every year (2009:  $\chi^2 = 25.01$ ,  $df = 2$ ,  $P < 0.001$ ; 2010:  $\chi^2 = 25.41$ ,  $df = 2$ ,  $P < 0.001$ ; 2011:  $\chi^2 = 7.07$ ,  $df = 2$ ,  $P < 0.05$ ; 2012:  $\chi^2 = 9.04$ ,  $df = 2$ ,  $P < 0.05$ ). Specifically, in 2009, moderate plots had more attacks per tree than low ( $P < 0.05$ ) and non-burned ( $P < 0.001$ ) plots. In 2010, again moderate plots had more attacks per tree than low ( $P < 0.001$ ) and non-burned ( $P < 0.001$ ) plots. In 2011, moderate plots had more attacks per tree than non-burned plots ( $P < 0.05$ ). Finally, in 2012, moderate plots had more attacks per tree than non-burned plots ( $P < 0.05$ ).

At Upper Saskatchewan, neither the proportion of trees attacked nor the number of attacks per tree differed among years, but they both differed among fire injury classes (proportion:  $F_{1.98, 116.77} = 15.38$ ,  $P < 0.001$ ; attacks:  $F_{1.96, 113.68} = 14.96$ ,  $P < 0.001$ ; Fig. 2.2). Specifically, non-burned plots had proportionally fewer trees attacked than both low ( $P < 0.001$ ) and moderate ( $P < 0.05$ ) plots. Similarly, non-burned plots had fewer attacks per tree than both low ( $P < 0.001$ ) and moderate ( $P < 0.05$ ) plots.

At the Ya Ha Tinda Ranch, neither the proportion of trees attacked nor the number of attacks per tree differed among years, but they both differed among fire injury classes (proportion:  $F_{1.94, 46.10} = 8.40$ ,  $P < 0.001$ ; attacks:  $F_{1.93, 47.30} = 8.24$ ,  $P < 0.001$ ; Fig. 2.3). Specifically, moderate plots had proportionally more trees attacked than non-burned plots ( $P < 0.001$ ). Similarly, moderate plots had more attacks per tree than non-burned plots ( $P < 0.001$ ).

Relationships described at the plot level coincide with those at the tree level. Beetle attack at the tree level was best predicted by bole and duff char in 2009 and 2010, by bole char and bole char height in 2011, and by bole char alone in 2012 (Table 2.2). Bole and duff char were always positive predictors of attack, while bole char height was negative.

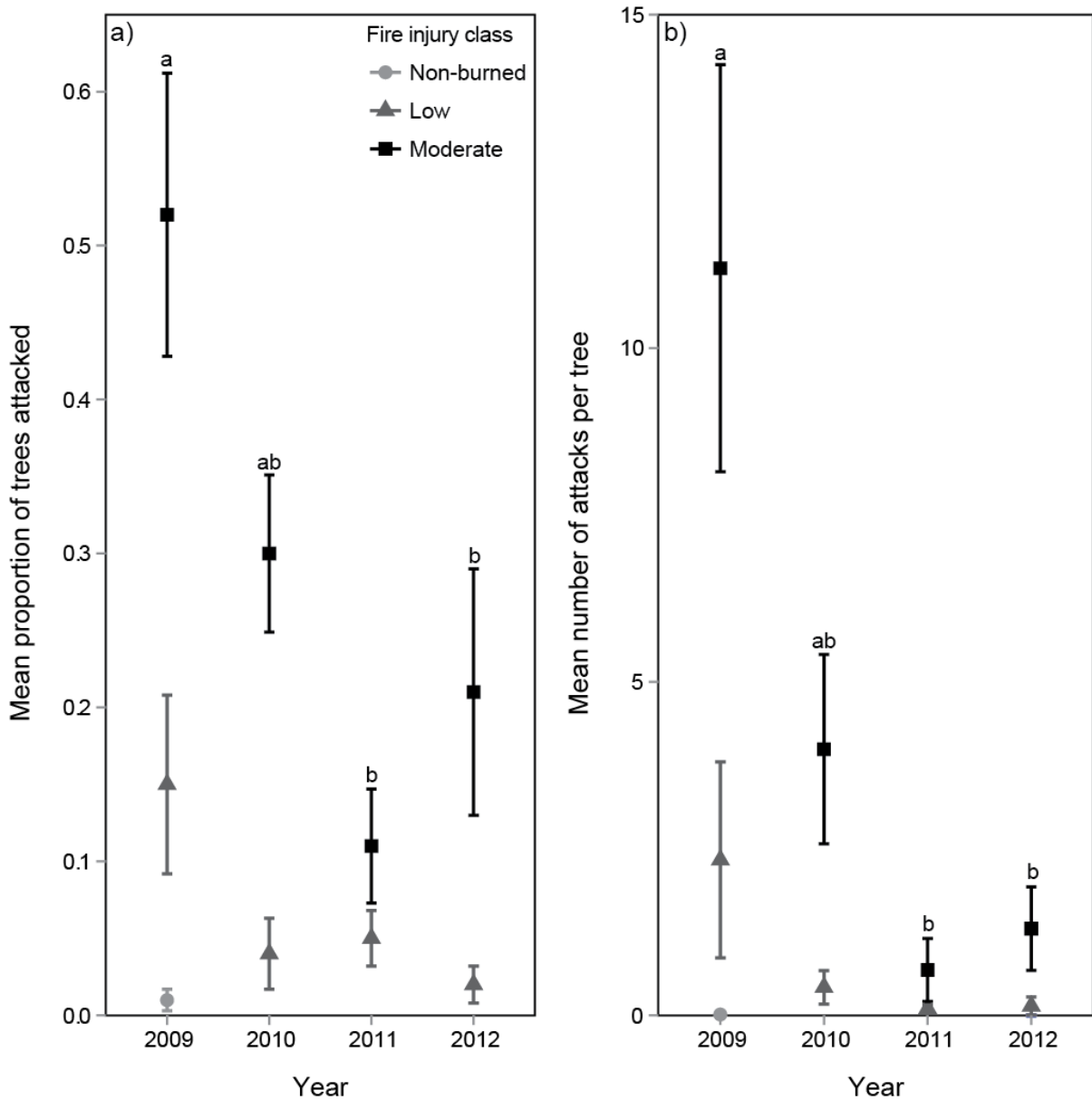


Figure 2.1: Non-cumulative, mean ( $\pm$  SE) per plot a) proportions of *Dendroctonus ponderosae*-attacked *Pinus contorta* trees and b) number of attacks per tree within three fire injury classes for 4 years at Mt. Nestor. Sample sizes at the start of the study are as follows: non-burned, 158 trees and 15 plots; low, 162 and 16; moderate, 107 and 14. A prescribed fire occurred in spring 2009. Different letters denote significant differences among years, where year was treated as a main effect, i.e., all data were used, regardless of class ( $\alpha = 0.05$ ). Differences among classes were investigated in each year individually after a significant interaction was found. See text for details.

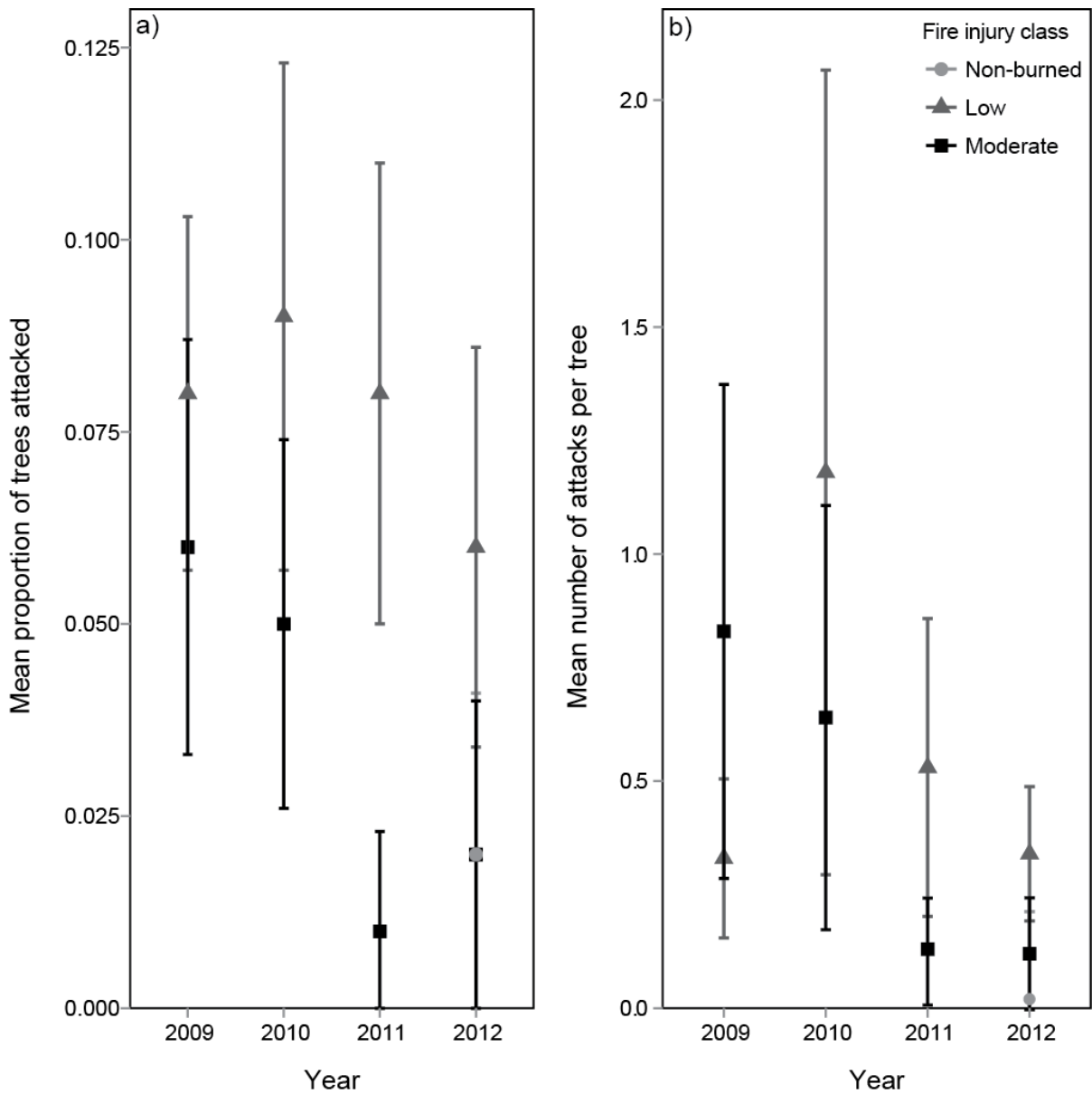


Figure 2.2: Non-cumulative, mean ( $\pm$  SE) per plot a) proportions of *Dendroctonus ponderosae*-attacked *Pinus contorta* trees and b) number of attacks per tree within three fire injury classes for 4 years at Upper Saskatchewan. Sample sizes at the start of the study are as follows: non-burned, 175 trees and 16 plots; low, 210 and 19; moderate, 96 and 15. A prescribed fire occurred in spring 2009. There were no differences among years, but there were differences among classes for both proportion of trees attacked and number of attacks per tree (both  $P < 0.001$ ). See text for details.

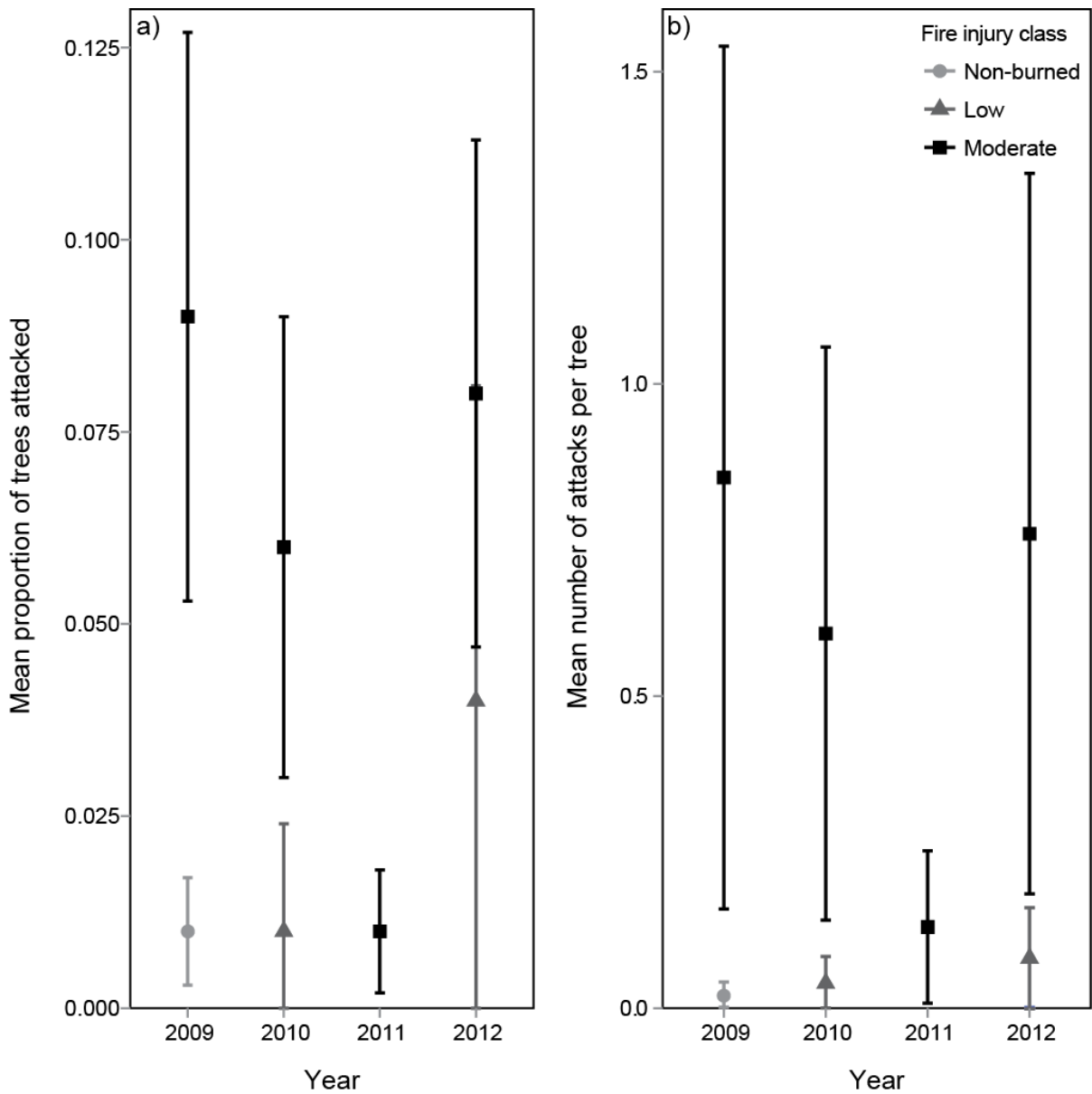


Figure 2.3: Non-cumulative, mean ( $\pm$  SE) per plot a) proportions of *Dendroctonus ponderosae*-attacked *Pinus contorta* trees and b) number of attacks per tree within three fire injury classes for 4 years at the Ya Ha Tinda Ranch. Sample sizes at the start of the study are as follows: non-burned, 134 trees and 15 plots; low, 63 and 7; moderate, 180 and 23. A prescribed fire occurred in spring 2009. There were no differences among years, but there were differences among classes for both proportion of trees attacked and number of attacks per tree (both  $P < 0.001$ ). See text for details.

Table 2.2: Estimates of the four models that best predicted *Dendroctonus ponderosae* attack of *Pinus contorta* trees each year, using bole char, bole char height, and duff char as predictors. These data pertain to three prescribed fires that occurred in spring 2009.

Model parameters	Year	n	Coefficient	Z	P
bole char	2009	808	0.02	1.84	0.066
duff char			0.02	2.20	0.028
duff char	2010	796	0.02	2.14	0.033
bole char	2011	592	0.06	2.44	0.015
bole char height			-0.29	-1.60	0.111
bole char	2012	465	0.02	1.95	0.051

### 2.3.2 Post-fire tree mortality

At Mt. Nestor, rates of tree death differed among years ( $F_{1.67, 81.21} = 8.44, P < 0.001$ ; Fig. 2.4a), where rates in 2012 were lower than those in 2010 ( $P < 0.05$ ). Because I found an interaction between fire injury class and year ( $F_{3.27, 81.21} = 4.59, P < 0.01$ ; Fig. 2.4a), I looked at the main effect of fire injury class for each year separately. Rates of tree death differed among fire injury classes in every year (Kruskal-Wallis; 2010:  $\chi^2 = 26.87, df = 2, P < 0.001$ ; 2011:  $\chi^2 = 9.42, df = 2, P < 0.01$ ; 2012:  $\chi^2 = 7.59, df = 2, P < 0.05$ ). Specifically, in 2010, moderate plots had greater rates of tree death than both low ( $P < 0.01$ ) and non-burned ( $P < 0.001$ ) plots. In 2011, non-burned plots had lower rates of tree death than both low ( $P < 0.05$ ) and moderate ( $P < 0.05$ ) plots. Finally, in 2012, moderate plots had greater rates of tree death than non-burned plots ( $P < 0.05$ ).

At Upper Saskatchewan, rates of tree death differed among years ( $F_{1.70, 92.49} = 14.94, P < 0.001$ ; Fig. 2.4b), where rates in 2012 were lower than those in both 2010 ( $P < 0.01$ ) and 2011 ( $P < 0.01$ ). Because I found an interaction between fire injury class and year ( $F_{3.17, 92.49} = 3.73, P < 0.05$ ; Fig. 2.4b), I looked at the main effect of fire injury class for each year separately. Rates of tree death differed among fire injury classes in every year (Kruskal-Wallis; 2010:  $\chi^2 = 19.08, df = 2, P < 0.001$ ;

2011:  $\chi^2 = 27.88$ ,  $df = 2$ ,  $P < 0.001$ ; 2012:  $\chi^2 = 12.78$ ,  $df = 2$ ,  $P < 0.01$ ). Specifically, in 2010, moderate plots had greater rates of tree death than both low ( $P < 0.05$ ) and non-burned ( $P < 0.001$ ) plots. In 2011, non-burned plots had lower rates of tree death than both low ( $P < 0.001$ ) and moderate ( $P < 0.001$ ) plots. Finally, in 2012, moderate plots had greater rates of tree death than non-burned plots ( $P < 0.01$ ).

At the Ya Ha Tinda Ranch, rates of tree death differed among years ( $F_{1.73, 32.53} = 5.56$ ,  $P < 0.05$ ; Fig. 2.4c), where rates in 2012 were lower than those in 2011 ( $P < 0.05$ ). Rates of tree death also differed among fire injury classes ( $F_{1.80, 32.53} = 12.08$ ,  $P < 0.001$ ; Fig. 2.4c), where non-burned plots had lower rates than both low ( $P < 0.05$ ) and moderate ( $P < 0.001$ ) plots.

### 2.3.3 Phloem quality

Total N concentration differed among fire injury classes 1 year ( $F_{2, 43} = 5.94$ ,  $P < 0.01$ ; Fig. 2.5) and 3 years ( $F_{2, 43} = 3.34$ ,  $P < 0.05$ ; Fig. 2.5) after fire; burned trees generally had a greater concentration. Specifically, 1 year after fire, non-burned trees had a lower concentration than moderate trees ( $P < 0.01$ ), but had a similar concentration to low trees. Three years after fire, non-burned trees tended to have less phloem N than low trees (marginally significant:  $P = 0.059$ ), but had a similar concentration to moderate trees. Phloem moisture did not differ among injury classes, either 1 or 3 years after fire. Phloem thickness did not differ among injury classes.

## 2.4 Discussion

I found that fire-injured trees are more susceptible to attack from low-density populations of *D. ponderosae*, but that prescribed fires merely provide a short-term increase in attack, a result only revealed by multi-year data. I thus demonstrate that prescribed

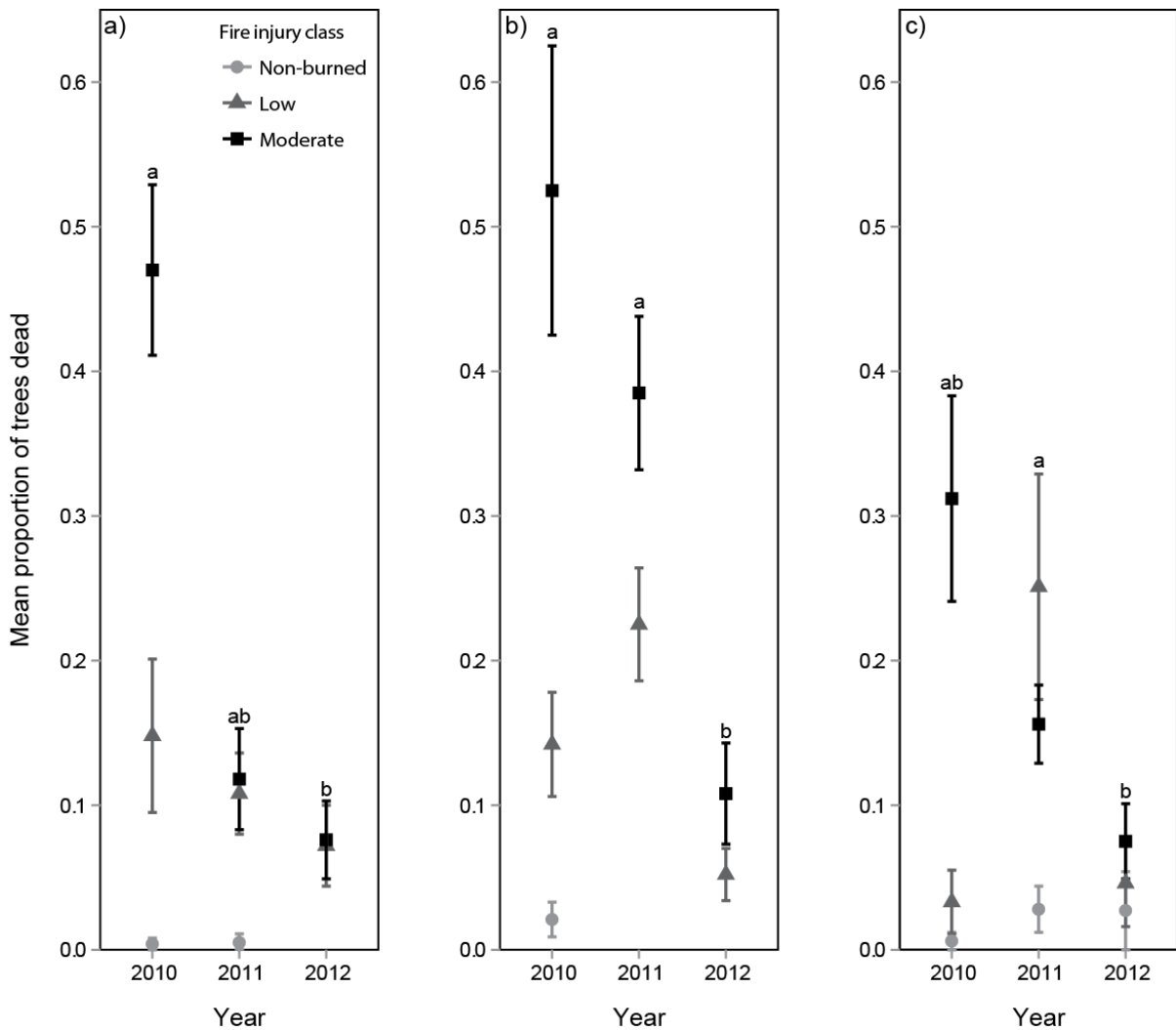


Figure 2.4: Non-cumulative, mean ( $\pm$  SE) proportions of dead *Pinus contorta* trees per plot at a) Mt. Nestor (sample sizes at the start of the study are as follows: non-burned, 158 trees and 15 plots; low, 162 and 16; moderate, 107 and 14), b) Upper Saskatchewan (non-burned, 175 trees and 16 plots; low, 210 and 19; moderate, 96 and 15), and c) the Ya Ha Tinda Ranch (non-burned, 134 trees and 15 plots; low, 63 and 7; moderate, 180 and 23) within three fire injury classes for 3 years after fire. Prescribed fires occurred in spring 2009. Different letters denote significant differences among years ( $\alpha = 0.05$ ). There were significant differences among fire injury classes at all sites. See text for details.

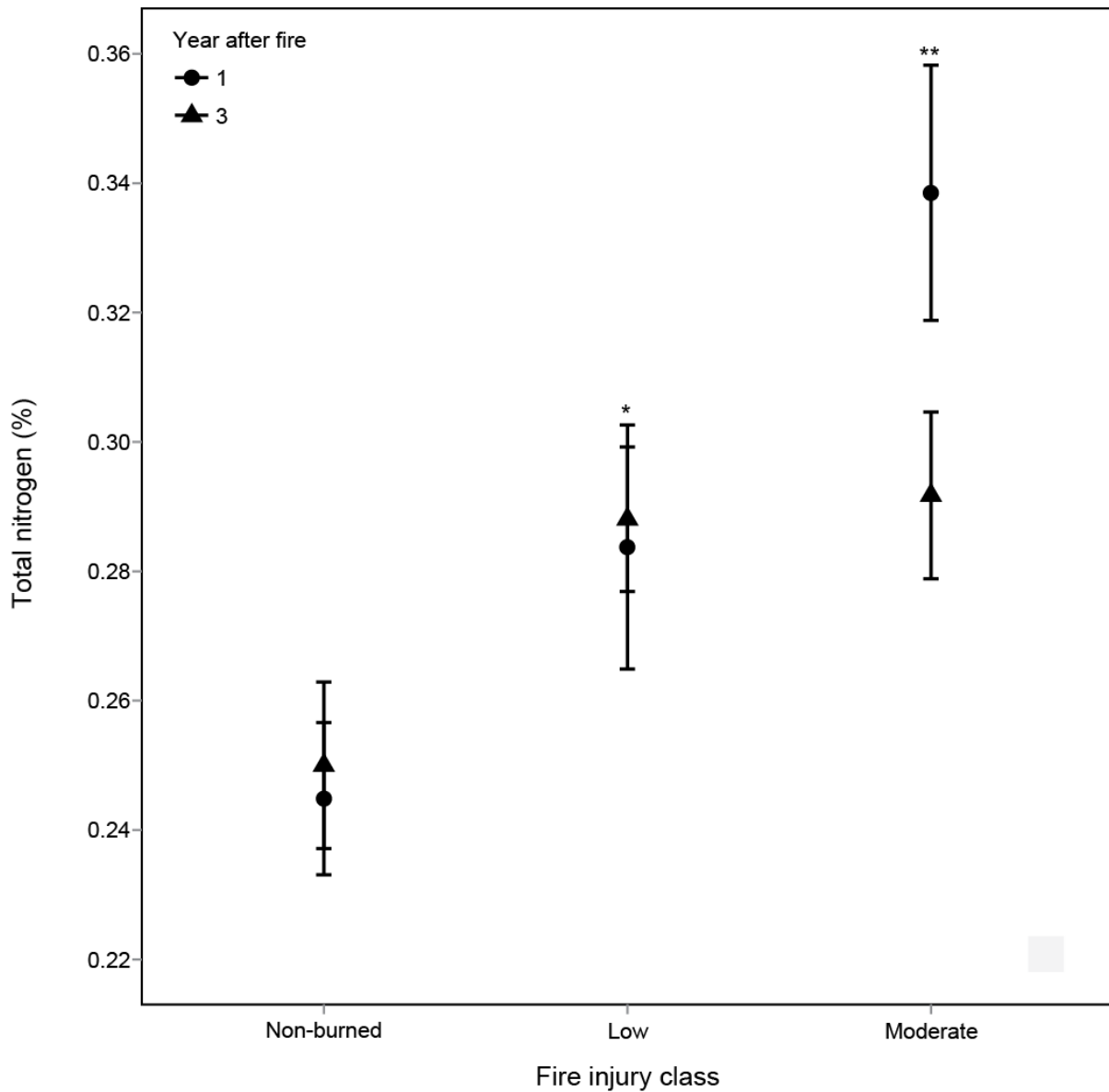


Figure 2.5: Mean total nitrogen ( $\pm$  SE) concentrations per plot of *Pinus contorta* phloem in three fire injury classes, 1 and 3 years after fire. Sample sizes are as follows: 1 year after fire, 33 non-burned trees, 29 low, 22 moderate; 3 years after fire, 27, 39, 24. Information regarding classes is provided in materials and methods. Tests were performed within years. A single asterisk (\*) indicates a marginally significant difference ( $P = 0.059$ ; among 3-year-post-fire samples), and a double asterisk (\*\*) indicates a significant difference ( $P < 0.05$ ; among 1-year-post-fire samples) from the non-burned controls of the individual time categories.



fire likely does not cause low-density populations of *D. ponderosae* to shift into their potentially ecosystem-altering outbreak phase.

#### **2.4.1 Fire-injured *Pinus contorta* show increased susceptibility to *Dendroctonus ponderosae***

My results at all sites show that low-density populations of *D. ponderosae* attacked proportionally more burned than non-burned trees, with more attacks per tree, in post-fire *P. contorta* stands, in agreement with earlier studies (e.g., Geiszler et al. 1984; Powell et al. 2012). Powell et al. (2012) found that eruptive populations also prefer attacking burned trees. Further, beetles generally attacked proportionally more moderately burned than lightly burned trees. These results are consistent with *D. ponderosae*-host tree interactions at low-density population levels, when beetles generally attack stressed trees (Safranyik et al. 2010). Fire injury may increase susceptibility by lowering host tree chemical defences (Powell and Raffa 2011), their main protection against bark beetles (Raffa et al. 2008). In contrast, others found that fire-injured *P. contorta* are neither more attractive nor more susceptible to *D. ponderosae* (e.g., Amman and Ryan 1991; Elkin and Reid 2004). For example, Elkin and Reid (2004) observed no difference in *D. ponderosae* colonisation between burned and non-burned trees. However, they burned single trees, which may not have provided enough cues, like infrared radiation or volatile chemicals, to signal weakened trees (Evans 1966; Schütz et al. 1999).

I assessed bole char, bole char height, and duff char as predictors of *D. ponderosae* attack on *P. contorta*. Only bole char positively predicted beetle attack 4 consecutive years after fire, supporting an earlier report of a positive relationship between the proportion of bark beetle-attacked trees and bole damage after fire (Geiszler et al. 1984). I suspect that bole char may have altered tree defences against bark beetles

(Powell and Raffa 2011). Duff char, representing fine root damage, positively predicted attack only immediately after fire, likely because trees with severe root damage died and were not available as hosts. Finally, bole char height negatively predicted beetle attack only 2 years after fire. High bole char indicates extensive phloem charring, and since *D. ponderosae* does not attack charred phloem (Elkin and Reid 2004), these trees may not provide enough resources for successful attack and reproduction.

#### **2.4.2 Post-fire *Pinus contorta* stands do not promote outbreaks of *Dendroctonus ponderosae***

Burned *P. contorta* stands in this study provided only temporary, pulsed resources for low-density *D. ponderosae* populations, a trend that was clearest at Mt. Nestor. Although beetles attacked proportionally more burned than non-burned trees every year, the incidence of attack either decreased, as at Mt. Nestor, or remained very low, as at Upper Saskatchewan and the Ya Ha Tinda Ranch. For example, the proportion of attacked trees was reduced from 22% in 2009 to 10% in 2011 (averaged across all sites). Furthermore, neither the proportion of trees attacked, nor the number of attacks per tree, increased in non-burned plots over time. Thus, our results from all sites suggest that fire does not promote *D. ponderosae* outbreaks, and are generally similar to those of Davis et al. (2012), who reported a reduction in bark beetle attack 2 years after fire in a *P. ponderosa* forest.

Two long-standing competing hypotheses predict that post-fire stands either promote outbreaks (Rasmussen et al. 1996; McHugh et al. 2003) or provide only short-term resources, perhaps culminating in refugia for low-density populations (Miller and Patterson 1927; Powell et al. 2012). Both assume that beetles preferentially attack fire-injured trees, which has been shown (e.g., Powell et al. 2012), but longer-term trends of post-fire beetle attack have been lacking. Studies addressing *D. ponderosae* attack

only 1 year after fire (e.g., Safranyik et al. 2001; Elkin and Reid 2004; Powell et al. 2012; Kulakowski and Jarvis 2013), although valuable in examining the susceptibility of fire-injured trees, have predicted contradictory trajectories for beetle populations over time. Our study is one of the few focussed on long-term beetle attack trends, and thus our results are valuable to understanding variation in beetle populations within burned stands. To this end, if I had observed attacks for just 1 year, when beetle colonisation was relatively high at Mt. Nestor, I may have erroneously predicted the stands would become population sources.

### **2.4.3 Potential mechanisms**

I tested two hypotheses to explain the decline in beetle attack over time in some post-fire stands. First, I tested whether resource quality changes over time and found that with respect to phloem N concentrations, burned trees always represented an equal or better quality resource than non-burned trees, contrary to the conclusions of Powell et al. (2012). Since organic matter mineralises during fire, studies have reported increases in ammonium and nitrate—important N sources for many plants—in post-fire soils (Wan et al. 2001). Shenoy et al. (2013) found increased nitrate uptake by *Picea mariana* even 16 years after fire, demonstrating the role of fire in long-term nutrient uptake by surviving trees. Surviving *P. contorta* may also take advantage of newly available soil N after fire, elevating phloem N. In addition, phloem moisture in fire-injured trees was similar to that of non-burned trees, both 1 and 3 years after fire. This provides evidence against the hypothesis that burned trees will become too dry for colonisation (DeNitto et al. 2000), at least for 3 years after fire. Together, our phloem N and moisture results indicate that reduced resource quality is likely not the main mechanism explaining beetle attack decline in post-fire *P. contorta* stands. However, an important caveat to this assertion is that I did not test phloem quality of the same trees over

time. It is possible that local environmental factors and microhabitats differed between our 1-year- and 3-year-post-fire stands, which may have differentially affected phloem quality.

In contrast, our results support the hypothesis that reduced resource quantity explains why I did not observe evidence of *D. ponderosae* outbreaks after fire, as the number of susceptible hosts rapidly declined in burned stands. Beetles attacked proportionally more moderately burned trees than lightly or non-burned trees; attack density also followed this pattern. However, moderately burned trees initially died faster than did less fire-injured trees, as more injured trees are more likely to die. For example, in the first year after fire, moderate plots at Mt. Nestor lost almost 50% of their trees on average, compared to 15% loss in low plots and 0.4% loss in non-burned plots. Tree mortality after fire is well-studied, wherein a combination of fire injury, insect activity, and diseases can kill trees (e.g., Hood et al. 2007; Woolley et al. 2012). Indeed, I saw secondary bark beetles, such as *Ips pini*, increase over time, potentially contributing to tree death. I therefore hypothesise that a rapid decline in resource quantity may have negatively affected *D. ponderosae* population growth, as emerging beetles were limited in finding suitable hosts, and bark beetles in general incur high mortality searching for hosts during dispersal (Raffa and Berryman 1980).

Natural conditions introduce complexity beyond the conditions of our study. Of our sites, only Mt Nestor had a beetle attack rate large enough for statistical comparisons among fire injury classes. Various factors can explain low beetle presence in the remaining sites, including in non-burned trees, such as beetle abundance prior to fire and topography, particularly elevation, aspect, and slope (Samman and Logan 2000; Safranyik and Carroll 2006; Faccoli and Bernardinelli 2014). I also speculate that differences in burn size may have affected observations, as Mt. Nestor was the smallest burn (618 ha vs. 1,264 ha and 4,632 ha). Beetles may have spread out further in the

larger burns and the likelihood of finding attacked trees was thus higher in the smaller burn: a potential “dilution effect”. There are no reports of how burn size affects bark beetle attraction, but due to its critical implications for bark beetle management, this issue deserves further investigation.

#### 2.4.4 Conclusions

Bark beetles are the focus of many studies investigating the large-scale drivers of ecosystem processes, population dynamics, and subsequent disturbances (Veblen et al. 1994; Turner et al. 1997; Elkin and Reid 2004; Kurz et al. 2008; Powell et al. 2012). In this study, I show that although *D. ponderosae* attacks more burned than non-burned trees, colonisation either remains low or decreases over time after a short resource pulse, providing evidence that prescribed fire does not promote *D. ponderosae* outbreaks. To determine the ultimate fates of beetles in post-fire *P. contorta* stands, future research should determine long-term reproductive success within burned areas. Although our study focussed only on prescribed fires, a recent study by Powell et al. (2012) found similar results 1 year after a wildfire. However, wildfires may have a higher proportion of high severity areas (Pollet and Omi 2002) due to their occurrence during peak burning season when vegetation is drier, and may show different long-term colonisation patterns. Further, while preference for fire-injured stands is preserved (Powell et al. 2012), post-fire colonisation patterns differ depending on population size; thus, research tracking eruptive populations in post-fire habitats over multiple years is needed. Post-fire *D. ponderosae* colonisation has been previously reported, but predominantly using single year surveys and often yielding contradictory results. I suggest that longer-term studies are necessary to understanding such complex ecological interactions, so that trends are fully apparent. Though bark beetle research seems especially pressing during outbreaks, understanding the ecology of low-density popula-

tions is a vital prerequisite to understanding how and why they shift to outbreak levels. Because fire does not seem to promote primary bark beetle outbreaks and may decrease populations over time, I recommend the continued use of prescribed fire for the general management of *P. contorta* forests with low-density *D. ponderosae* populations.

## Chapter 3

# Competitors and natural enemies may cumulatively mediate *Dendroctonus ponderosae* colonisation of burned *Pinus* forests

### 3.1 Introduction

Fire is an important component of many forest ecosystems in North America, influencing nutrient cycles, regeneration, and productivity, and interacting with other major biotic disturbance agents, such as insects, to influence the landscape (Bonan and Shugart 1989; Jenkins et al. 2008). Fire can affect insect communities both directly and indirectly via plants, and shapes their community structure and species diversity (Kim and Holt 2012). Because their host trees often sustain extensive fire injuries, subcortical insects, which feed on the subcortical tissues of their hosts, are especially affected. For example, a number of studies have focussed on bark beetles (Curculionidae: Scolyt-

inae), as they are abundant in recent burns (e.g., Amman and Ryan 1991; Rasmussen et al. 1996; Santoro et al. 2001; McHugh et al. 2003; Six and Skov 2009), and can alter forest structure, nutrient cycles, and plant species composition by causing extensive mortality during periodic outbreaks (Kurz et al. 2008; Bentz et al. 2010; Raffa et al. 2013). *Dendroctonus ponderosae* Hopkins (mountain pine beetle), the most economically and ecologically significant insect species in western North American conifer forests (Amman and Baker 1972; Li et al. 2005), is termed a primary bark beetle because it can kill healthy host trees when its populations are sufficiently large (Lindgren and Raffa 2013). *Dendroctonus ponderosae* can develop in several pines, including *Pinus contorta* (lodgepole pine), a seral species that frequently has serotinous cones and depends on fire for reproduction (Muir and Lotan 1985).

Western North American conifer forests have historically been shaped by fire and insect disturbances (Romme and Knight 1982) and thus fire and *D. ponderosae* have a complex relationship. *Dendroctonus ponderosae* causes extensive and relatively rapid *P. contorta* mortality, increasing fuel loads and the potential for fire (Jenkins et al. 2008; but see Page et al. 2014 for a critical review of predictive fire models). Conversely, the beetles appear to preferentially attack fire-injured trees (Stock and Gortley 1989; Powell et al. 2012; Chapter 2 of this thesis), presumably taking advantage of weakened tree defences resulting from physiological stress (Raffa and Berryman 1987). As such, past studies have proposed that fire may promote primary bark beetle outbreaks (Rasmussen et al. 1996; Kulakowski and Jarvis 2013), wherein many otherwise healthy hosts are injured in a short period of time. For example, Rasmussen et al. (1996) found high levels of bark beetle infestation in fire-injured *Pseudotsuga menziesii* (Douglas-fir) and *P. contorta*, and suggested that this may increase the infestation of uninjured trees. Likewise, Kulakowski and Jarvis (2013) found that fire-injured *P. contorta* were more likely to be attacked by *D. ponderosae*, proposing that low-severity fires



may increase forest susceptibility to outbreaks. However, in a recent study (Chapter 2 of this thesis), I found that although endemic-level (low-density population) *D. ponderosae* preferentially attacked fire-injured *P. contorta* every year for 4 years after prescribed fire, overall attack rates decreased substantially over time. Because colonisation of burned stands changed over time only among burned plots, not among non-burned control plots, I believe that it was affected by changes within the burn, and not by external influences such as climate or *D. ponderosae* population dynamics at the landscape level. This suggests that prescribed fire can create a short-term resource pulse, similar to that found by Davis et al. (2012) in *Pinus ponderosa* (ponderosa pine) forests. Thus, determining the mechanisms driving the decline in colonisation following the resource pulse, and keeping beetle attacks low over time, is critical to understanding endemic-level populations of primary bark beetles and, by extension, their outbreak dynamics in burned stands.

*Dendroctonus ponderosae* responses to fire-injured hosts are most likely mediated by community interactions, as the beetles are associated with a diverse subcortical insect community of competitors, predators, and parasitoids, that may influence their numbers at endemic population levels (Safranyik and Carroll 2006; Boone et al. 2008). Some secondary bark beetles, which generally only attack dead or dying trees, and other wood-boring insects are attracted to fire-injured hosts. For example, *Ips pini*, a common secondary bark beetle in North America and a direct competitor with *D. ponderosae* in *P. contorta* forests (Rankin and Borden 1991), increases in burned forests (Amman and Ryan 1991; Santoro et al. 2001). In addition, wood borers in the family Buprestidae can be abundant in post-fire stands (Schütz et al. 1999). *Dendroctonus ponderosae* is a poor competitor (Rankin and Borden 1991; Safranyik and Carroll 2006), especially at endemic population levels, so I hypothesised that increased competition in burned areas may limit its ability to reach outbreak levels.

Although past studies have reported elevated insect populations after prescribed fire and wildfire, they have generally focussed on abundant species, such as bark beetles (e.g., Geiszler et al. 1984: *D. ponderosae* and *I. pini*; Amman and Ryan 1991: mainly *Dendroctonus pseudotsugae*, *Dendroctonus rufipennis* and *I. pini*; Rasmussen et al. 1996: mainly *D. pseudotsugae*, *D. rufipennis*, and *I. pini*; McHugh et al. 2003, *Dendroctonus adjunctus*, *Dendroctonus brevicomis*, *D. ponderosae*, *Dendroctonus valens*, and *Ips* spp.). Studies on species or families of rarer insects, such as hymenopteran parasitoids and dipteran predators, after fire, have generally received little attention or yielded unclear results (e.g., Six and Skov 2009; Powell et al. 2012). In particular, there have been no studies on the cumulative effects of natural enemies on bark beetle populations, although there are some reports of increased numbers of Hymenoptera and Diptera after prescribed fire (Six and Skov 2009). Since bark beetle natural enemies and competitors are both attracted to burned areas, their combined responses are likely important in exerting pressures on low density primary bark beetle populations, even when their individual effects are not. Therefore, comprehensive studies of communities, rather than individual species or families, are necessary for fully understanding the effects of host fire injury on subcortical insects.

I used a whole-community approach to assess the determinants of primary bark beetle colonisation of post-fire stands, while asking two questions: (1) What are the temporal and spatial colonisation patterns of the subcortical community after prescribed fire, and (2) can the subcortical community, particularly competitors and natural enemies of bark beetles, affect *D. ponderosae* colonisation of burned stands? I addressed these questions in the *P. contorta* forests of Alberta, Canada, in 2010–2012, while *D. ponderosae* were at low-density population levels. These areas have recently been exposed to a *D. ponderosae* outbreak, and lie within long-term forest management regions that include prescribed fire. Thus, examining the interactions of primary

bark beetles and their natural enemies in post-fire forests is especially relevant in these stands.

## 3.2 Materials and methods

### 3.2.1 Study sites and fire-injury classes

I used three mature *P. contorta* forests within the Alberta Rocky Mountains, in which prescribed fires occurred in spring 2009. Please see Chapter 2 for details, including locations, size of burned areas, and fire cycles.

I used Parks Canada's burn severity classifications, based on US Geological Survey techniques (Soverel et al. 2010), to define three fire injury classes: non-burned, low, and moderate. These techniques use pre- and post-fire images from Landsat Thematic Mapper data. I used ArcGIS 9.2 (ESRI, Redlands, CA, U.S.A.) to randomly locate at least 15  $10 \times 10$  m plots, a minimum of 200 m apart to avoid clumping, throughout each fire injury class at each site. Plots were spread throughout each burn and average nearest neighbour distances between plots were 233 m at Mt. Nestor, 256 m at the Ya Ha Tinda Ranch, and 439 m at Upper Saskatchewan. I did not use high fire injury classes as these contained no live trees, and thus no available hosts for *D. ponderosae* attack. I performed ground-truthing to ensure that Parks Canada's aerial classifications were precise enough to be used on the ground, where fire injuries vary on a finer scale than is discernible from the air. I visually estimated bole char (the percentage of the trunk that was charred) for each tree in our plots as a general measure of fire injury, and averaged these values per plot to define fire injury classes. Non-burned, low, and moderate on the Parks Canada scale corresponded to 0% bole char, 1–15% bole char (mean across all plots and sites 10.86%), and  $\geq 16\%$  bole char (mean 31.42%), respectively. Within each plot, I individually tagged all live *P. contorta* trees  $> 15$  cm

Table 3.1: Summaries of bole char (the percentage of each trunk that was charred), duff char (the percentage of the forest floor organic layer that was burned in a 1-m-diameter circle around the base of each tree), and bole char height (the maximum height of the charred area on each trunk) for three sites (Mt. Nestor, the Ya Ha Tinda Ranch, Upper Saskatchewan), divided among fire injury classes. Information regarding classes is provided in materials and methods. All means are  $\pm$  SE, where SE was determined using the number of plots as sample size. n/a = not applicable.

	Nr. Plots	Nr. Trees	Mean DBH (cm)	Mean bole char (%)	Mean duff char (%)	Mean bole char height (m)
<b>Mt. Nestor</b>						
Non-burned	15	158	22.96 $\pm$ 1.52	n/a	n/a	n/a
Low	16	162	25.03 $\pm$ 1.53	8.65 $\pm$ 1.04	80.62 $\pm$ 4.35	1.28 $\pm$ 0.17
Moderate	14	107	25.17 $\pm$ 1.69	28.89 $\pm$ 2.17	94.21 $\pm$ 2.33	3.55 $\pm$ 0.23
<b>Ya Ha Tinda</b>						
Non-burned	15	134	27.76 $\pm$ 1.72	n/a	n/a	n/a
Low	7	63	23.78 $\pm$ 1.85	11.33 $\pm$ 1.13	81.53 $\pm$ 6.22	2.31 $\pm$ 0.30
Moderate	23	180	26.02 $\pm$ 0.95	29.22 $\pm$ 1.95	95.90 $\pm$ 1.32	5.21 $\pm$ 0.29
<b>Upper Saskatchewan</b>						
Non-burned	16	175	24.12 $\pm$ 1.55	n/a	n/a	n/a
Low	19	210	22.32 $\pm$ 1.16	8.19 $\pm$ 0.99	81.91 $\pm$ 4.07	1.48 $\pm$ 0.20
Moderate	15	96	23.03 $\pm$ 1.30	36.14 $\pm$ 5.12	97.66 $\pm$ 1.01	6.42 $\pm$ 1.03

in diameter at breast height (DBH; *D. ponderosae* generally attacks larger trees), and measured diameter and phloem thickness at breast height. Summaries of various fire injury characteristics for each class are provided in Table 3.1.

### 3.2.2 *Dendroctonus ponderosae* attacks and subcortical insect collection

To determine annual *D. ponderosae* activity, I quantified beetle attacks in each plot for 4 consecutive years (2009–2012). Attacks were determined by the presence of pitch tubes (exuded sap) and frass (a mixture of insect faeces and boring dust), which I counted only above 1 m on the trunk (up to  $\sim$ 5 m) to avoid erroneously including lower-stem colonising beetles. Typically, *D. ponderosae* leaves unique entry marks characterised by yellow pitch tubes. Red boring dust may be found in bark crevices and at the base of the tree. If I were unsure of an entry mark, I removed a small portion

of outer bark (done rarely for only ~5 trees in each burn) and observed tunnelling (*D. ponderosae* maternal and larval galleries are distinctive). Trees were generally not killed by *D. ponderosae*.

To survey subcortical insect species I used three types of passive traps (i.e., without attractants), intended to capture a wide variety of families: emergence (Fig. 3.1), landing (Fig. 3.2), and flight intercept (Fig. 3.3). At all sites for 3 consecutive years (2010–2012), I placed 3–5 traps of each type in each of the fire injury classes from late May to late August of each year, and collected trapped insects only at the end of each trapping period. Emergence traps were created by wrapping a 1 × 2 m fine mesh cloth (mesh size < 0.5 mm) with a hanging 2-m cloth funnel (made by cutting the cloth into a large V-shape) around the trunk of a tree, at a height of between 1 and 2 m. To the bottom of each cloth funnel, I attached a 105 mL urine sample cup, filled with 10 mL of 50% propylene glycol solution diluted with water, using a standard pipe clamp. To collect trapped insects, cups were simply removed from their clamps and sealed. Landing traps were made by cutting the bottom from a plastic 2 L soda bottle, and then cutting the bottle in half length-wise. Lids were glued to the inverted tops of the bottles, which became funnels. To each lid, I attached a 105 mL plastic sample cup filled with 10 mL of 50% propylene glycol solution, diluted with water. Traps were then attached to tree trunks at breast height (~1.3 m), using staples. To collect insects in the field, cups were removed as for emergence traps. Finally, flight intercept panel traps (Advanced Pheromone Technologies, Marylhurst, OR, U.S.A.), were hung between two trees at least 1 m off the ground, using rope. Collection cups were filled with 50 mL of 50% propylene glycol solution, diluted with water. To collect trapped insects, cups were removed from the bottoms of the traps and the liquid poured into 1-L Nalgene bottles (Thermo Fisher Scientific Inc., Waltham, MA, U.S.A.). Flight intercept traps were left in the same locations year to year, landing traps were always placed on

live trees, and were moved only if trees had died over the winter, and emergence traps were always moved to new trees within the same plot to avoid excluding insects.

Traps were sorted following field collection, and insects were initially separated by taxonomic order and stored in vials filled with 70% ethanol. Subsequently, I identified families known to include subcortical insect species from three orders: Coleoptera (beetles), Hymenoptera (wasps), and Diptera (flies). I identified 5,243 individuals of the subcortical community to 31 Families, as well as one sub-family (Scolytinae), based on potential interactions with *D. ponderosae* reported in the literature (e.g., Kenis et al. 2004). These were then divided among three functional groups—competitors, predators, and parasitoids—based on their potential associations with *D. ponderosae*. I separated predators and parasitoids because they have distinct effects on bark beetles and their attraction patterns differ; e.g., predators are attracted before parasitoids to trees colonised by bark beetles (Amman 1984; Reeve 1997; Boone et al. 2008). For the purposes of discussing family-level analyses, I will be referring to Scolytinae as a family.

### **3.2.3 Statistical analyses**

All statistical analyses were performed using R version 3.0.2 (R Development Core Team 2013). Any family occurring in < 5% of traps in any given analysis was removed from that analysis (Table 3.2). All abundances were then standardised to account for differences in the number of trapping days. To visualise the effects of fire injury class and year on the subcortical communities at each site, I used Nonmetric Multidimensional Scaling (NMDS; *ecodist* package in R), an ordination method well-suited to community data with many zeroes (McCune and Grace 2002). This method requires a distance measure, with which a dissimilarity matrix is built; I chose the Bray-Curtis dissimilarity for its usefulness with ecological abundance data. Distances



Figure 3.1: The author setting up an emergence trap to passively trap insects emerging from under the bark of trees.



Figure 3.2: A landing trap, used to passively catch flying insects that attempt to land on tree trunks.





Figure 3.3: A flight intercept trap, used to passively catch flying insects.

between samples are then ranked and represented in a low-dimensional configuration that minimises stress, a measure of the configuration's success at displaying more similar points closer together. Typically, using more axes will lower stress but confound interpretability, and Zuur et al. (2007) suggested that when stress values exceed 0.3, additional axes should be considered.

I used NMDS analyses for two types of data: insect families and functional groups (predators, parasitoids, and competitors). I performed a separate analysis at each site for each type of data, for a total of 6 NMDS analyses. Additionally, I used Permutational Multivariate Analyses of Variance (PerMANOVA; *ecodist* package in R) to test the responses of the subcortical communities at each site to fire injury class and year, along with any interactions between the two. PerMANOVA allows non-normal community data to be tested, comparing groups by calculating a test statistic that represents the ratio of distances among groups to distances within groups. As above, I used the Bray-Curtis dissimilarity for distance calculations. I also used PerMANOVAs to test the association of the subcortical communities at each site with *D. ponderosae* presence and year, plus any interactions between the two. Because of their strong correlation, I did not use fire injury class and *D. ponderosae* presence in the same tests. I checked all data for multivariate homogeneity of group dispersions before implementing PerMANOVAs (*vegan* package in R). Finally, I used permutational ANOVA tests (*lmPerm* package in R) to determine the effects of fire injury class, year, and/or *D. ponderosae* presence on each of the functional groups individually at each site. This allowed us to determine which of the insect families and groups contributed most to each of the community results.

Table 3.2: The subcortical insect families identified and enumerated in this study. Insects were trapped at three sites (Mt. Nestor, the Ya Ha Tinda Ranch, and Upper Saskatchewan) for 3 consecutive years after fire. Check marks indicate which families were used for Non-metric Multidimensional Scaling (NMDS) analyses at the family and functional group levels.

	Mt. Nestor		Ya Ha Tinda		Upper Sask.		All sites	
	Family	Group	Family	Group	Family	Group	Family	Group
<b>Competitors</b>								
<i>Order Coleoptera</i>								
Buprestidae				✓		✓		
Cerambycidae	✓	✓	✓	✓	✓	✓	✓	✓
Scolytinae (sub-family)	✓	✓	✓	✓	✓	✓	✓	✓
<i>Order Hymenoptera</i>								
Siricidae		✓	✓	✓	✓	✓		✓
<b>Predators</b>								
<i>Order Coleoptera</i>								
Cleridae	✓	✓	✓	✓	✓	✓	✓	✓
Staphylinidae	✓	✓	✓	✓	✓	✓	✓	✓
Trogossitidae		✓		✓	✓	✓	✓	✓
<i>Order Diptera</i>								
Asilidae			✓	✓		✓		✓
Dolichopodidae		✓	✓	✓	✓	✓	✓	✓
Empididae	✓	✓	✓	✓	✓	✓	✓	✓
Lonchaeidae		✓	✓	✓	✓	✓	✓	✓
Xylophagidae				✓				✓
<b>Parasitoids</b>								
<i>Order Hymenoptera</i>								
Braconidae		✓	✓	✓	✓	✓	✓	✓
Ceraphronidae	✓	✓	✓	✓	✓	✓	✓	✓
Chalcididae		✓						✓
Cynipidae						✓		✓
Diapriidae		✓	✓	✓	✓	✓	✓	✓
Encyrtidae				✓		✓		✓
Eucharitidae						✓		✓
Eucoilidae				✓				✓
Eulophidae		✓		✓		✓		✓
Eupelmidae						✓		✓
Eurytomidae			✓	✓		✓		✓
Ichneumonidae	✓	✓	✓	✓	✓	✓	✓	✓
Liopteridae				✓				✓
Megaspilidae				✓				✓
Mymaridae				✓		✓		✓
Platygastridae	✓	✓	✓		✓		✓	
Proctotrupidae	✓		✓		✓		✓	
Pteromalidae	✓	✓	✓	✓	✓	✓	✓	
Scelionidae	✓	✓	✓	✓	✓	✓	✓	
Torymidae					✓		✓	

### 3.3 Results

I found no differentiation between low and moderate fire injury classes with respect to the insect community. I thus combined these, resulting in two fire injury classes: burned and non-burned. All statistical analyses were performed on these two classes. Overall, I used 50 and 32 traps in burned and non-burned stands, respectively, in 2010, 49 and 34 traps in 2011, and 62 and 30 traps in 2012.

#### 3.3.1 Responses of subcortical insect families to fire-injured hosts

Overall, NMDS analyses showed that insect families were associated with burned areas (Figs. 3.4–3.6, a only) and later years following fire, although there was no clear differentiation between 2 and 3 years after fire (Figs. 3.4–3.6, b only). Standardised means of all families are provided in Table 3.3. At Mt. Nestor (Fig. 3.4; two axes, stress < 0.3), all insect families, except Ichneumonidae (Hymenoptera), were associated with burned areas. Similarly, all insect families except Ichneumonidae were associated with 2 and 3 years after fire, while traps collected 1 year after fire were more dispersed throughout the NMDS space. The family Ichneumonidae does not appear to be associated with any class or year. Instead, I saw consistently few ichneumonids in all traps (Table 3.3). At the Ya Ha Tinda Ranch (Fig. 3.5; two axes, stress = 0.3), as with Mt. Nestor, most insect families, except Scelionidae, Diapriidae, Braconidae (Hymenoptera), and Dolichopodidae (Diptera), were associated with burned areas. Patterns among years were unclear but traps collected 1 year after fire were again more variable in their positions in the NMDS plots. At Upper Saskatchewan (Fig. 3.6; two axes, stress < 0.3), there were again associations between all insect families and burned areas. This site showed the clearest association between insect families and traps collected 2 and 3 years after fire.

With respect to fire injury and year following fire, PerMANOVA results showed that the subcortical community as defined by insect families was different between classes and generally different among years after fire, but only one site showed an interaction between the two (Table 3.4). At Mt. Nestor, the community only differed between fire injury classes. At both Upper Saskatchewan and the Ya Ha Tinda Ranch, the community differed both between classes and among years following fire, and there was an interaction between fire injury class and year at the Ya Ha Tinda Ranch.

With respect to *D. ponderosae* presence and year following fire, PerMANOVA results of the subcortical community as defined by insect families showed no clear trend among sites (Table 3.5). *Dendroctonus ponderosae* presence significantly affected the community only at Mt. Nestor, and year affected the community only at Upper Saskatchewan. No sites showed an interaction between *D. ponderosae* presence and year following fire. However, I could not include year in our analysis at the Ya Ha Tinda Ranch because of difficulty achieving homogeneity of group dispersion.

### **3.3.2 Responses of insect functional groups to fire-injured hosts**

In general, NMDS analyses showed that all three functional groups (predators, parasitoids, and competitors) were associated with burned areas (Figs. 3.7–3.9, a only). Similarly, functional groups were generally associated with later years following fire, although there was no clear differentiation between 2 and 3 years after fire (Figs. 3.7–3.9, b only). Standardised means of all functional group abundances are provided in Table 3.6 and graphically in Fig. 3.10. At Mt. Nestor (Fig. 3.7; two axes, stress < 0.3), all competitors and predators were associated with burned areas. Parasitoids, however, were not clearly associated with fire. All three groups were associated with 2 and 3 years after fire. At the Ya Ha Tinda Ranch (Fig. 3.8; two axes, stress < 0.3), all three functional groups were associated with the burned area, but there

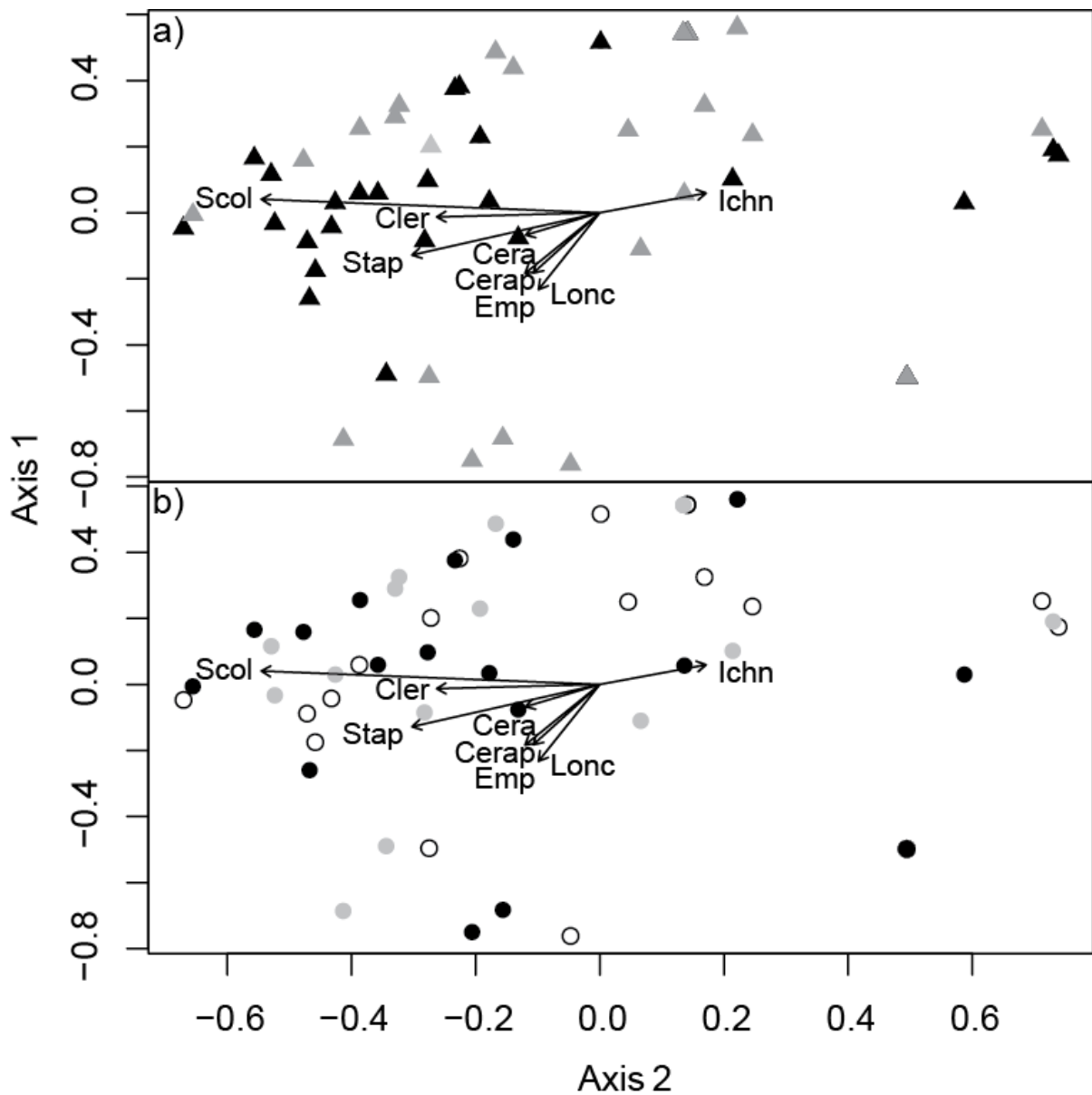


Figure 3.4: Visualisation of the effects of a) fire injury (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on the subcortical community as defined by insect families at Mt. Nestor, using Nonmetric Multidimensional Scaling (NMDS). a) Black filled triangles represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open circles represent traps collected 1 year after fire, grey filled circles represent traps collected 2 years after fire, and black filled circles represent traps collected 3 years after fire. Cera = Cerambycidae, Scol = Scolytinae, Cler = Cleridae, Stap = Staphylinidae, Emp = Empididae, Lonc = Lonchaeidae, Cerap = Ceraphronidae, Ichn = Ichneumonidae.

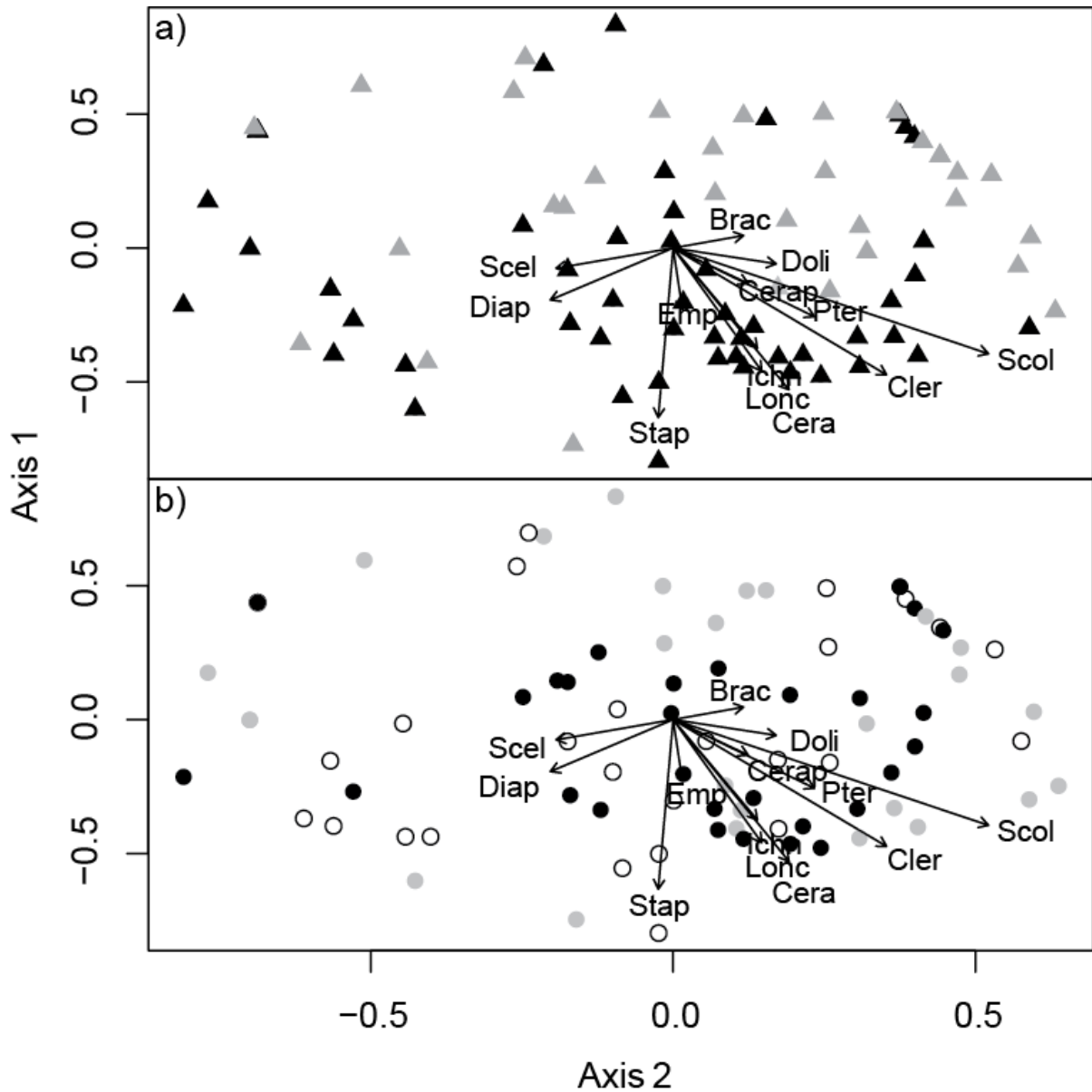


Figure 3.5: Visualisation of the effects of a) fire injury (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on the subcortical community as defined by insect families at the Ya Ha Tinda Ranch, using Nonmetric Multidimensional Scaling (NMDS). a) Black filled triangles represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open circles represent traps collected 1 year after fire, grey filled circles represent traps collected 2 years after fire, and black filled circles represent traps collected 3 years after fire. Cera = Cerambycidae, Scol = Scolytinae, Cler = Cleridae, Stap = Staphylinidae, Doli = Dolichopodidae, Emp = Empididae, Lonc = Lonchaeidae, Brac = Braconidae, Cera = Ceraphronidae, Diap = Diapriidae, Ichn = Ichneumonidae, Pter = Pteromalidae, Scel = Scelionidae.

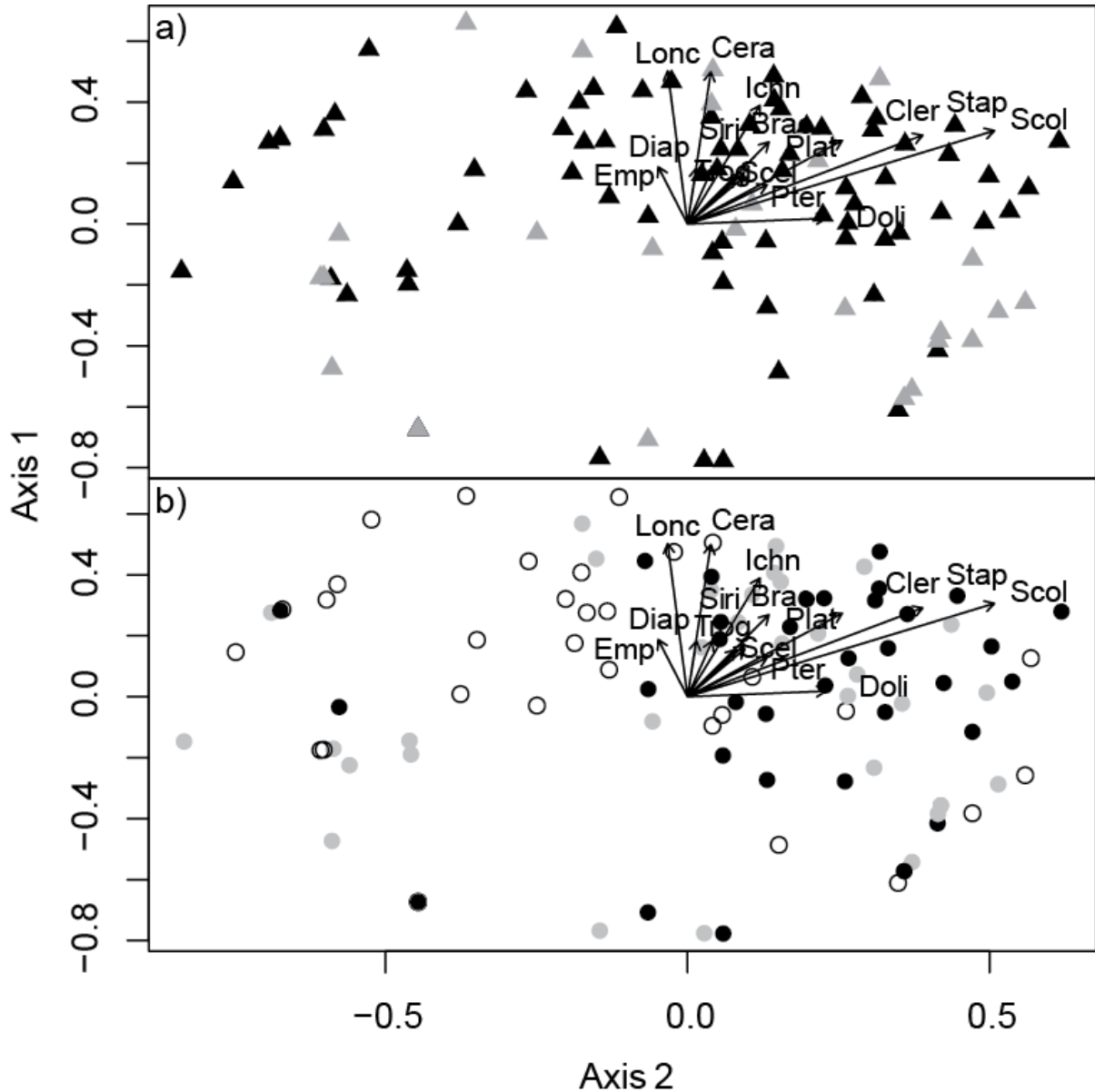


Figure 3.6: Visualisation of the effects of a) fire injury (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on the subcortical community as defined by insect families at Upper Saskatchewan, using Nonmetric Multidimensional Scaling (NMDS). a) Black filled triangles represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open circles represent traps collected 1 year after fire, grey filled circles represent traps collected 2 years after fire, and black filled circles represent traps collected 3 years after fire. Cera = Cerambycidae, Scol = Scolytinae, Siri = Siricidae, Cler = Cleridae, Stap = Staphylinidae, Trog = Trogossitidae, Doli = Dolichopodidae, Emp = Empididae, Lonc = Lonchaeidae, Bra = Braconidae, Diap = Diapriidae, Ichn = Ichneumonidae, Plat = Platygastriidae, Pter = Pteromalidae, Scel = Scelionidae.





Table 3.4: Results of three Permutational Analyses of Variance (PerMANOVA), depicting the effects of year after fire (3 years) and fire injury class (burned and non-burned) on the subcortical community as defined by insect families at each of three study sites: Mt. Nestor, the Ya Ha Tinda Ranch, and Upper Saskatchewan. \* denotes significant effects at  $\alpha = 0.05$ .

Site	Variable	DF	F	P
Mt. Nestor	Year	2	0.17	0.958
	Fire Injury	1	8.17	0.005*
	Year $\times$ Fire injury	2	1.74	0.135
Ya Ha Tinda Ranch	Year	2	2.12	0.012*
	Fire injury	1	3.99	0.001*
	Year $\times$ Fire injury	2	1.72	0.032*
Upper Saskatchewan	Year	2	2.68	0.001*
	Fire injury	1	4.19	0.002*
	Year $\times$ Fire injury	2	1.33	0.172

Table 3.5: Results of three Permutational Analyses of Variance (PerMANOVA), depicting the effects of year after fire (3 years) and *Dendroctonus ponderosae* presence on the subcortical community as defined by insect families at each of three study sites: Mt. Nestor, the Ya Ha Tinda Ranch, and Upper Saskatchewan. \* denotes significant effects at  $\alpha = 0.05$ .

Site	Variable	DF	F	P
Mt. Nestor	Year	2	0.18	0.965
	<i>D. ponderosae</i> presence	1	4.24	0.025*
	Year $\times$ <i>D. ponderosae</i>	2	0.83	0.462
Ya Ha Tinda Ranch	<i>D. ponderosae</i> presence	1	0.32	0.828
Upper Saskatchewan	Year	2	3.95	0.005*
	<i>D. ponderosae</i> presence	1	1.55	0.167
	Year $\times$ <i>D. ponderosae</i>	2	1.90	0.084

was no clear association with any year after fire. At Upper Saskatchewan (Fig. 3.9; two axes, stress < 0.3), all functional groups were again associated with burned areas and later years post-fire; there was some evidence for a stronger association with 3 years after fire than with 2 years after fire. With respect to fire injury class and year following fire, PerMANOVA results showed that the subcortical community as defined by functional groups was different between fire-injury classes and generally different among years, and that no sites showed interactions between classes and years (Table 3.7). Specifically, at Upper Saskatchewan, the community differed between fire-injury classes and years following fire. However, at Mt. Nestor and the Ya Ha Tinda Ranch, the community only differed between classes. Permutational ANOVA results showed that at Mt. Nestor, the community difference between classes was mostly driven by a difference in competitors ( $P < 0.01$ ). At the Ya Ha Tinda Ranch, both competitors and predators differed between fire injury classes (both  $P < 0.05$ ). Although the three functional groups defining the community as a whole did not differ among years after fire, competitors individually did ( $P < 0.05$ ). When the effect of year was analysed separately among competitors, the group differed only between 2010 and 2011 ( $P < 0.05$ ). At Upper Saskatchewan, the community difference between fire injury classes was mostly driven by predator differences ( $P < 0.01$ ), while the community differences among years after fire were mostly driven by competitor differences ( $P < 0.05$ ). When the effect of year was analysed separately among competitors, the group differed only between 2010 and 2012 ( $P = 0.01$ ).

With respect to *D. ponderosae* presence and year following fire, PerMANOVA results for the subcortical community as defined by insect groups showed mostly no differences (Table 3.8). *Dendroctonus ponderosae* presence no longer significantly affected the communities, and year affected the community only at Upper Saskatchewan. No sites showed an interaction between *D. ponderosae* presence and year following fire.

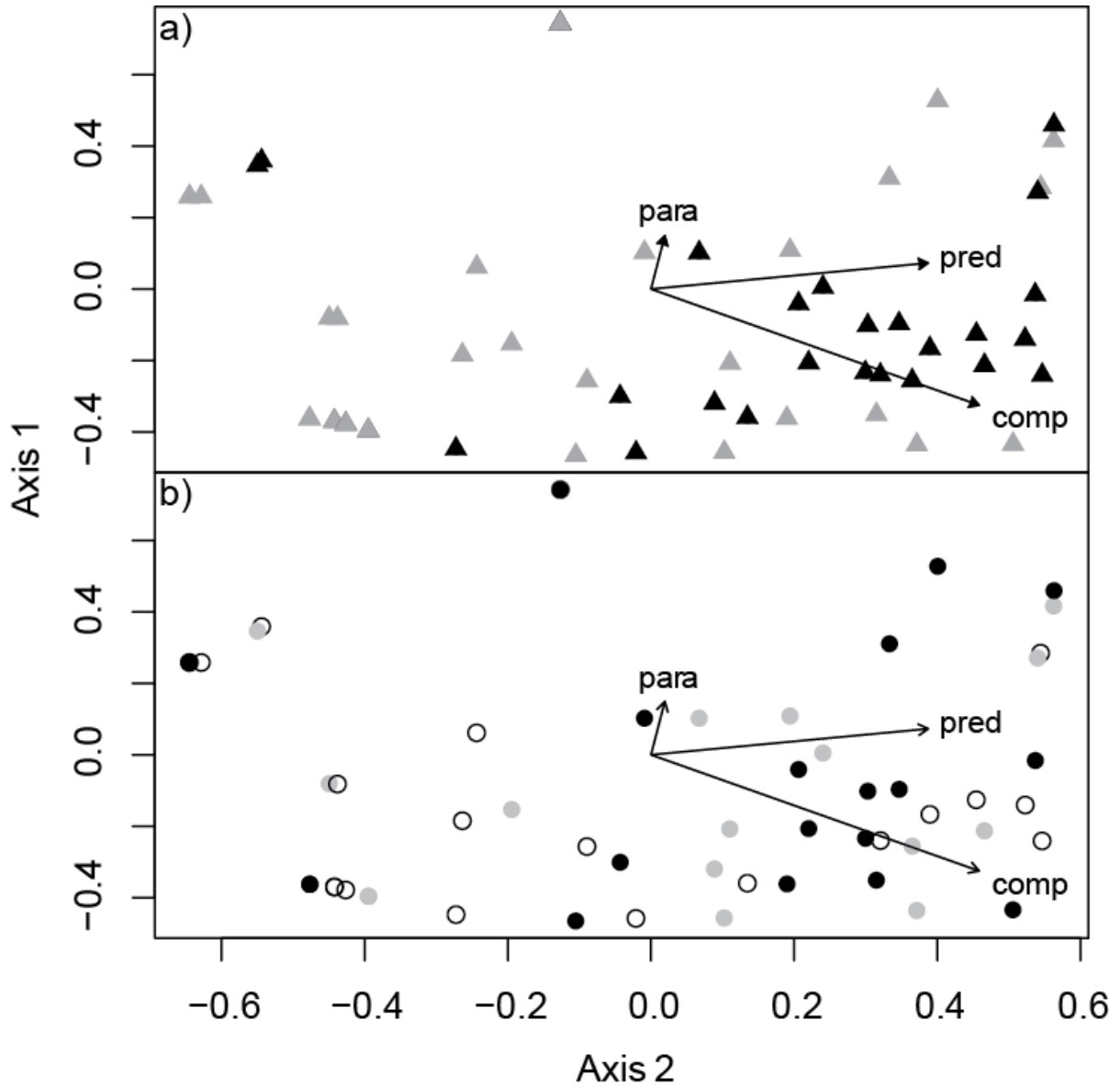


Figure 3.7: Visualisation of the effects of a) fire injury (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on the subcortical community as defined by insect functional groups at Mt. Nestor, using Nonmetric Multidimensional Scaling (NMDS). a) Black filled triangles represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open circles represent traps collected 1 year after fire, grey filled circles represent traps collected 2 years after fire, and black filled circles represent traps collected 3 years after fire. para = parasitoids, pred = predators, comp = competitors.

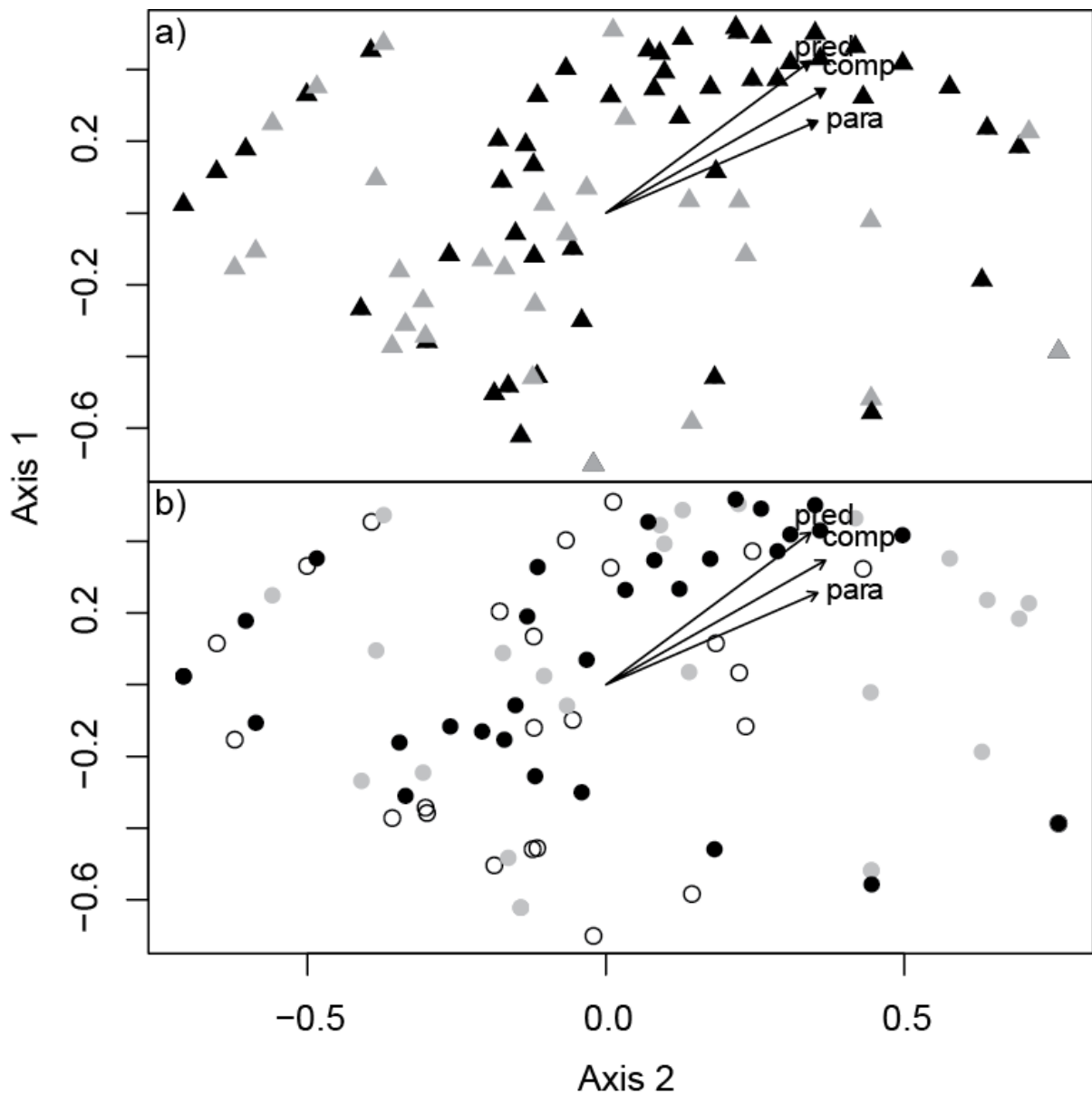


Figure 3.8: Visualisation of the effects a) fire injury class (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on the subcortical community as defined by insect functional groups at the Ya Ha Tinda Ranch, using Nonmetric Multidimensional Scaling (NMDS). a) Black filled triangles represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open circles represent traps collected 1 year after fire, grey filled circles represent traps collected 2 years after fire, and black filled circles represent traps collected 3 years after fire. para = parasitoids, pred = predators, comp = competitors.

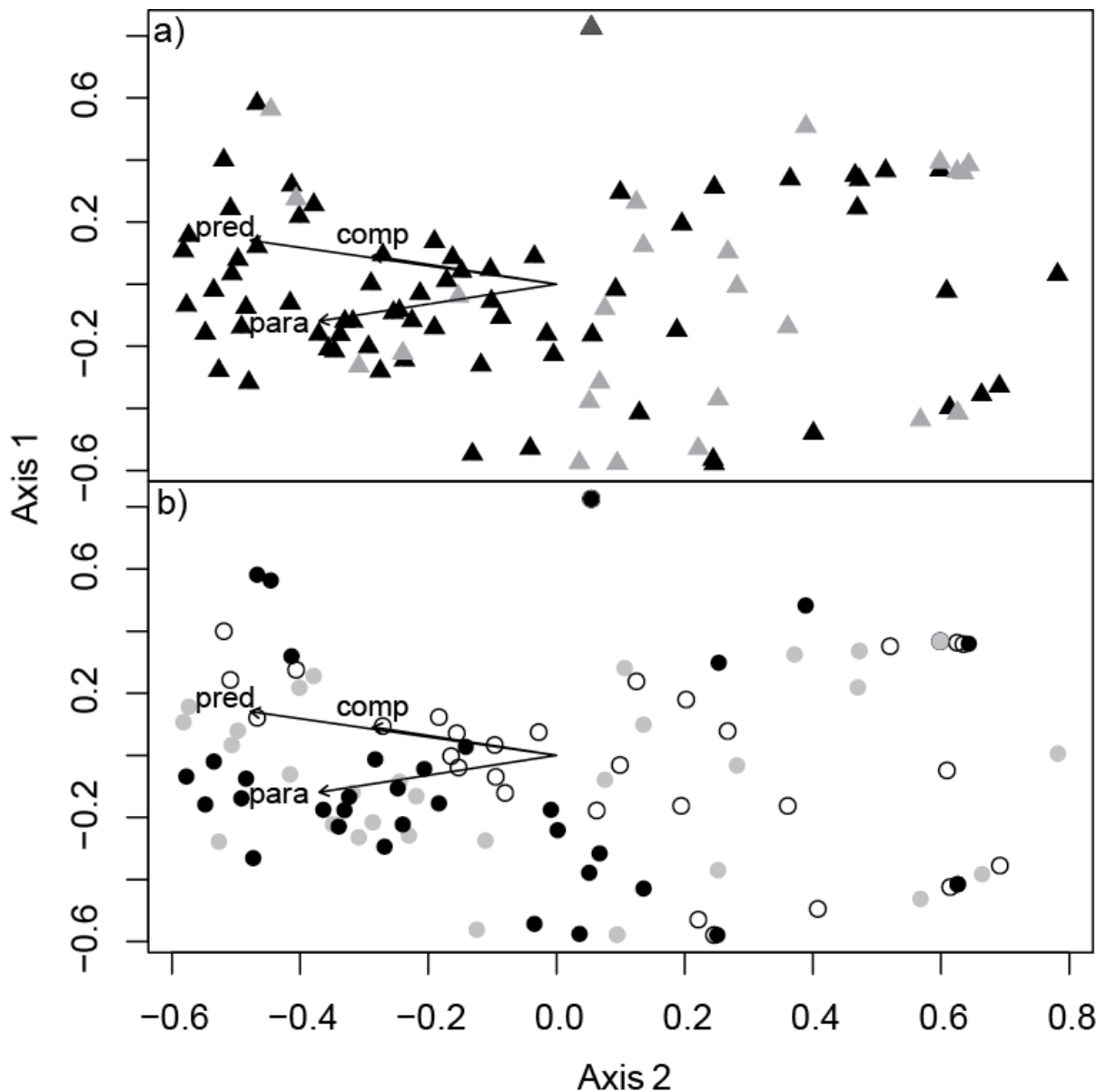


Figure 3.9: Visualisation of the effects of a) fire injury class (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on the subcortical community as defined by insect functional groups at Upper Saskatchewan, using Nonmetric Multi-dimensional Scaling (NMDS). a) Black filled triangles represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open circles represent traps collected 1 year after fire, grey filled circles represent traps collected 2 years after fire, and black filled circles represent traps collected 3 years after fire. para = parasitoids, pred = predators, comp = competitors.

Table 3.6: Standardized means (per trap day) of insect functional groups, divided among fire injury classes (non-burned, low, and moderate), sites, and years. 2010 refers to 1 year after fire, 2011 refers to 2 after fire, and 2012 refers to 3 years after fire. Ya Ha Tinda = Ya Ha Tinda Ranch, U. Saskatchewan = Upper Saskatchewan. Burned values are averages of those in the two fire injury classes. Competitors includes the families Buprestidae, Cerambycidae, Scolytinae, and Siricidae. Predators includes the families Cleridae, Staphylinidae, Trogossitidae, Asilidae, Dolichopodidae, Empididae, Lonchaeidae, and Xylophagidae. Parasitoids includes the families Braconidae, Ceraphronidae, Chalcididae, Cynipidae, Diapriidae, Encyrtidae, Eucharitidae, Eucoilidae, Eulophidae, Eupelmidae, Eurytomidae, Ichneumonidae, Liopteridae, Megaspilidae, Mymaridae, Platygasteridae, Proctotrupidae, Pteromalidae, Scelionidae, and Torymidae. Blank cells represent zero values.

Year	Site	Fire injury class	Competitors	Predators	Parasitoids
2010	Mt. Nestor	Non-burned	0.02	0.01	0.01
2010	Mt. Nestor	Low	0.12	0.02	
2010	Mt. Nestor	Moderate	0.10	0.06	0.01
2010	Mt. Nestor	Burned	0.11	0.04	0.01
2010	Ya Ha Tinda	Non-burned	0.03	0.04	0.01
2010	Ya Ha Tinda	Burned	0.07	0.13	0.02
2010	U. Saskatchewan	Non-burned	0.03	0.16	0.03
2010	U. Saskatchewan	Low	0.06	0.32	0.01
2010	U. Saskatchewan	Moderate	0.08	0.25	0.02
2010	U. Saskatchewan	Burned	0.07	0.29	0.02
2011	Mt. Nestor	Non-burned	0.03	0.01	0.01
2011	Mt. Nestor	Low	0.08	0.03	
2011	Mt. Nestor	Moderate	0.03	0.05	0.03
2011	Mt. Nestor	Burned	0.06	0.04	0.02
2011	Ya Ha Tinda	Non-burned	0.15	0.03	0.03
2011	Ya Ha Tinda	Burned	0.36	0.16	0.03
2011	U. Saskatchewan	Non-burned	0.07	0.05	0.02
2011	U. Saskatchewan	Low	0.27	0.29	0.04
2011	U. Saskatchewan	Moderate	0.19	0.34	0.03
2011	U. Saskatchewan	Burned	0.23	0.32	0.04
2012	Mt. Nestor	Non-burned	0.06	0.05	0.02
2012	Mt. Nestor	Low	0.07	0.07	0.01
2012	Mt. Nestor	Moderate	0.07	0.03	0.01
2012	Mt. Nestor	Burned	0.07	0.05	0.01
2012	Ya Ha Tinda	Non-burned	0.04	0.03	0.02
2012	Ya Ha Tinda	Burned	0.22	0.16	0.04
2012	U. Saskatchewan	Non-burned	0.53	0.06	0.04
2012	U. Saskatchewan	Low	0.28	0.22	0.04
2012	U. Saskatchewan	Moderate	0.90	0.27	0.03
2012	U. Saskatchewan	Burned	0.59	0.25	0.04

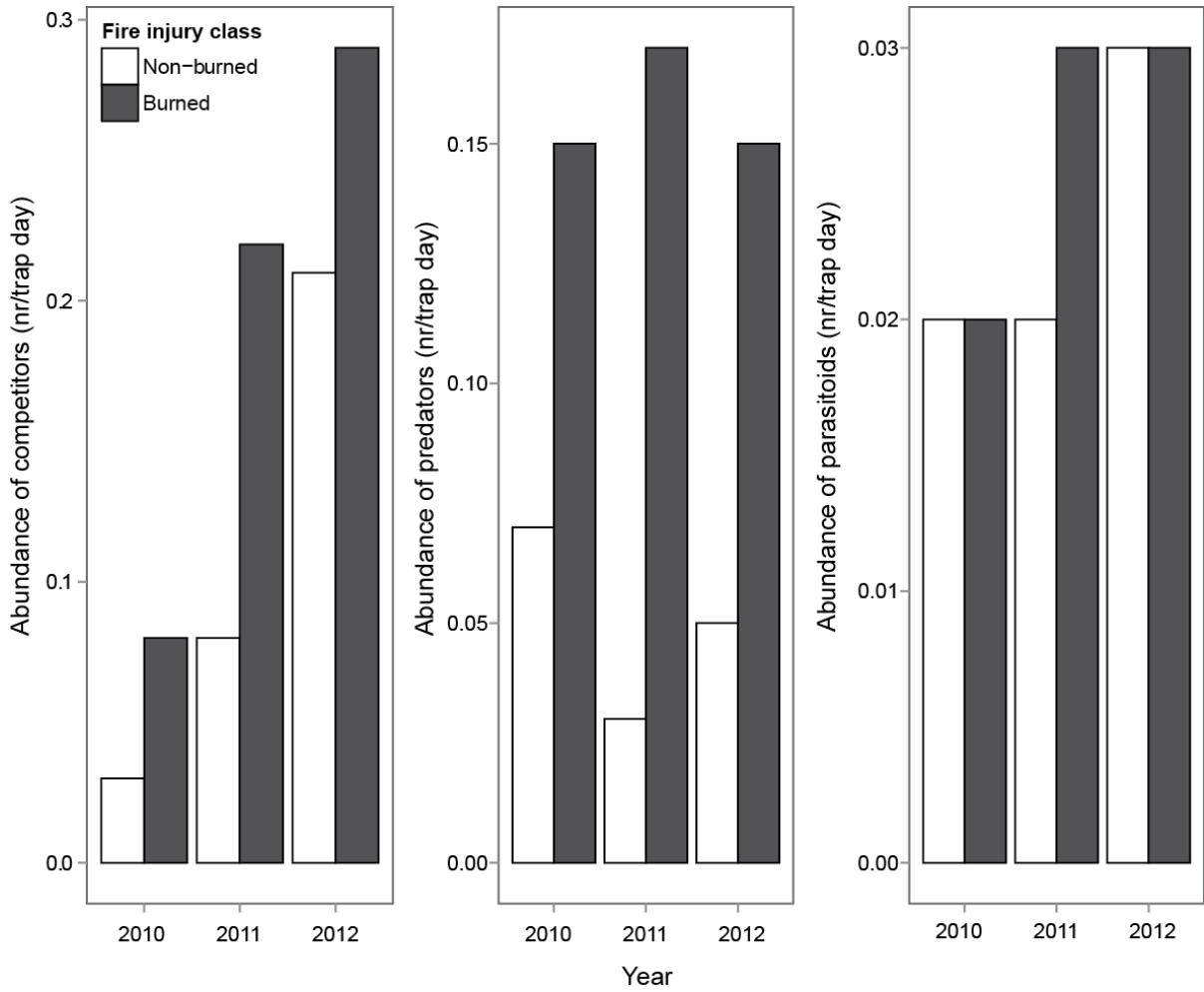


Figure 3.10: Standardised mean abundances (nr/trap day) of competitors, predators, and parasitoids, averaged across three sites (Mt. Nestor, the Ya Ha Tinda Ranch, and Upper Saskatchewan). Note that Y-axis scales differ.



Table 3.7: Results of three Permutational Analyses of Variance (PerMANOVA), depicting the effects of year after fire (3 years) and fire injury class (burned and non-burned) on the subcortical community as defined by insect functional groups (competitors, predators, and parasitoids) at each of three study sites: Mt. Nestor, the Ya Ha Tinda Ranch, and Upper Saskatchewan. \* denotes significant effects at  $\alpha = 0.05$ .

Site	Variable	DF	F	P
Mt. Nestor	Year	2	0.69	0.576
	Fire injury	1	7.63	0.003*
	Year $\times$ Fire injury	2	1.52	0.222
Ya Ha Tinda Ranch	Year	2	1.37	0.223
	Fire injury	1	6.69	0.002*
	Year $\times$ Fire injury	2	0.44	0.802
Upper Saskatchewan	Year	2	3.37	0.010*
	Fire injury	1	6.33	0.002*
	Year $\times$ Fire injury	2	0.51	0.770

Table 3.8: Results of three Permutational Analyses of Variance (PerMANOVA), depicting the effects of year after fire (3 years) and *Dendroctonus ponderosae* presence on the subcortical community as defined by insect functional groups (competitors, predators, and parasitoids) at each of three study sites: Mt. Nestor, the Ya Ha Tinda Ranch, and Upper Saskatchewan. \* denotes significant effects at  $\alpha = 0.05$ .

Site	Variable	DF	F	P
Mt. Nestor	Year	2	0.76	0.541
	<i>D. ponderosae</i> presence	1	1.69	0.140
	Year $\times$ <i>D. ponderosae</i>	2	0.68	0.538
Ya Ha Tinda Ranch	Year	2	1.47	0.185
	<i>D. ponderosae</i> presence	1	0.53	0.611
	Year $\times$ <i>D. ponderosae</i>	2	0.44	0.821
Upper Saskatchewan	Year	2	3.31	0.016*
	<i>D. ponderosae</i> presence	1	1.53	0.198
	Year $\times$ <i>D. ponderosae</i>	2	1.96	0.096

## 3.4 Discussion

Insect families and functional groups (predators, parasitoids, and competitors) were both more associated with burned than non-burned stands. The subcortical communities also varied among years, and were generally associated with 2 or 3 years after prescribed fire. Moreover, dissimilarities between burned and non-burned stands were driven by different subcortical communities at each site. Overall, our study provides the first evidence that competitors and natural enemies can potentially affect *D. ponderosae* colonisation of burned forests.

### 3.4.1 Differences between fire injury classes

The subcortical community, consisting of potential competitors, predators, and parasitoids of *D. ponderosae*, differed between burned and non-burned stands, and was predominantly associated with burns at all sites, whether I classified insects by family or functional group. Competitors were the most abundant functional group at all three sites, accounting for 51% of all insects identified over 3 years, and drove community differences between burned and non-burned stands at two sites. Many competitors take advantage of injured hosts in post-fire stands and our results are thus consistent with most existing accounts. Examples of increased competitor numbers after fire can be found for bark beetles (prescribed fire and wildfire; e.g., Bradley and Tueller 2001; Kelsey and Joseph 2003; Saint-Germain et al. 2004), wood borers (Cerambycidae and Buprestidae; wildfire and unknown fire type; Kelsey and Joseph 2003; Saint-Germain et al. 2004; Lombardero and Ayres 2011; Costello et al. 2013), and wood wasps (Siricidae; unknown fire type; Saint-Germain et al. 2004). Fire injury generally weakens tree host defences (Powell and Raffa 2011) and allows subcortical herbivores to colon-

ise even large, otherwise healthy trees. Indeed, some bark beetles have been observed to reach outbreak levels after fire (see review by McCullough et al. 1998).

Subcortical predators, including beetles and flies, comprised 41% of all identified insects and were also important in driving community differences between burned and non-burned stands at two sites. Predators of subcortical bark beetles are generally considered habitat specialists as they feed on several species (e.g., Erbilgin and Raffa 2001). They can also proliferate after fire, taking advantage of increased prey numbers. For example, studies have shown that predatory beetles in the families Cleridae (Santoro et al. 2001; Sanchez-Martinez and Wagner 2002; Kelsey and Joseph 2003) and Trogossitidae (Kelsey and Joseph 2003; Campbell et al. 2008), which prey on bark beetles, are associated with fire-injured hosts. Beetles in the family Staphylinidae can also prey on bark beetles and at least one staphylinid species has been reported to increase in scorched logs (Lombardero and Ayres 2011). Fly predators of bark beetles, such as *Medetera* spp. (Dolichopodidae), can increase after fire as well, presumably also taking advantage of increased prey abundance (Saint-Germain et al. 2004; Six and Skov 2009). Although flies in the family Asilidae are not specialised bark beetle predators, scolytins are among their prey (Dennis 1979). They, too, can increase in abundance after fire, although these interactions have not been well studied (McCravy and Baxa 2011). Some lonchaeid flies also prey on bark beetles (Wermelinger 2002), so they might also be expected to increase in abundance after fire along with their prey, but this association has not been previously reported in the literature. Although Lombardero and Ayres (2011) reported fewer *Lonchaea* spp. (Lonchaeidae) in scorched logs than in controls within 1 month of burning, I began collecting data 1 year after fire and found ~2–3 times more lonchaeid individuals in traps from non-burned areas than in those from burned areas, suggesting that these species respond to delayed fire injury cues.

Some hymenopteran parasitoid families and parasitoid functional groups were also associated with burned areas. Some parasitoids are attracted to cues emitted by bark beetle symbionts (Boone et al. 2008), and thus can take advantage of increased numbers of hosts in burned areas. However, possibly due to generally low abundances across all families, these associations were not critical in defining community differences between burned and non-burned stands, supporting an earlier study (Six and Skov 2009). Furthermore, my results are consistent with those of Mateos et al. (2011), who showed that most studied Mediterranean hymenopteran families were more numerous in post-burn areas 4 years after wildfire, in agreement with the general understanding that parasitoid communities are more diverse in complex landscapes (Langelotlo and Denno 2004).

### **3.4.2 Interactions between the subcortical community and *Dendroctonus ponderosae***

Community differences between areas with and without *D. ponderosae* demonstrate that subcortical communities can influence the population dynamics of *D. ponderosae* in burned stands. This was mostly evident at Mt. Nestor, likely because *D. ponderosae* populations were highest at this site (Chapter 2 of this thesis). I provide two lines of evidence to support this assertion. First, competitors and predators drove community differences in most study sites. Because *D. ponderosae* is a poor competitor (Rankin and Borden 1991; Safranyik and Carroll 2006), it is likely being outcompeted in areas with dense populations of other subcortical insect herbivores. Further, *D. ponderosae* is generally affected by various natural enemies (Safranyik and Carroll 2006), most of which increased in the burned stands over time, but remained relatively stable in non-burned stands. Second, I observed increases in the abundances of both competitors and predators after prescribed fire, which continued through time. Conversely, in an

accompanying study (Chapter 2 of this thesis) I observed that attacks from an endemic *D. ponderosae* population declined substantially 3 years after prescribed fire, particularly at Mt. Nestor. Thus, *D. ponderosae* is likely outcompeted as early as 1 year after fire and does not have enough time to build up populations in burned stands, which may reduce colonisation.

Notably, differences between areas with and without *D. ponderosae* were obscured when communities were divided into functional groups, indicating that community-level analyses of subcortical insects are sensitive to individual species abundances. Thus, species data should be collected whenever possible.

### **3.4.3 Temporal and spatial variation in subcortical communities**

Overall, communities were associated with later years after fire, but there was no differentiation between 2 and 3 years. Communities may have been saturated in terms of species abundance and composition within 2 years of fire due to sudden changes in habitat, and further changes may only be observed on a longer time scale as the vegetation recovers. Likewise, Werner (2002) found that cerambycids, buprestids, and scolytins were at similar abundances 5 and 10 years after disturbance, including prescribed fire, in Alaskan spruce forests.

Although fire injury affected the subcortical community at all sites, the groups driving these differences differed among sites. At Mt. Nestor, competitors were the most important; at the Ya Ha Tinda Ranch, both competitors and predators drove differences; and at Upper Saskatchewan, predators were most important. These results demonstrate the role of site-specific factors that may drive population dynamics of insects sharing the same habitat. For example, species composition, the age and size of host trees, and the densities of suitable hosts in a forest stand can all affect population dynamics of bark beetles (Samman and Logan 2000; Safranyik and Carroll 2006). Fur-

thermore, precipitation and temperature differences may contribute to community differences. For example, drought can negatively affect host tree defences and increased precipitation can positively affect competitors by increasing phloem moisture (Raffa et al. 2008). Temperature can affect multiple stages of insect life cycles, including development and reproduction (Six and Bentz 2007). The Ya Ha Tinda Ranch was the coldest site, with an average yearly temperature of  $-1.6^{\circ}\text{C}$  in 2010 (Alberta Agriculture and Rural Development), likely negatively affecting insect abundances. Topography, particularly elevation, aspect, and slope, varies widely and can also influence population dynamics of insect herbivores (Samman and Logan 2000; Safranyik and Carroll 2006; Faccoli and Bernardinelli 2014). For example, Mt. Nestor study plots fell on the steepest slopes, on average  $\sim 8^{\circ}$  steeper than those at other sites. Steep slopes can increase the incidence of disturbance from run-off, landslides, and soil slippage, which can negatively affect tree root health and thus predispose trees to insect attack (Samman and Logan 2000). Furthermore, the local abundance and composition of insects likely influences post-fire communities. Although fire may attract distant individuals, it is probable that local communities respond more strongly to sudden habitat changes.

#### **3.4.4 Conclusions**

Our study is the first to comprehensively describe the responses of a subcortical community to post-fire stands. Although the sudden change in environment affected the community for at least 2 years after prescribed fire, the extent of injury (low and moderate) did not appear to have an effect. This may indicate that the post-burn areas were too heterogeneous, at least during the first 3 years after fire that our study encompassed, such that clearly delineated areas of low and moderate burn either did not exist, or were too small to affect the habitat preferences of flying subcortical insects. Therefore, in our study, the post-burn stands as a whole caused a significant change in

the subcortical community. Furthermore, the change in the community continued up to 2 or 3 years after fire, depending on the site, especially when considering numbers of bark beetles and other wood borers. I thus emphasise the need for longer-term data in the study of post-fire ecological trends, even when looking at short-term effects.

# Chapter 4

## Fire-mediated interactions between a tree-killing bark beetle and its competitors

### 4.1 Introduction

Forest ecosystems are regulated by various abiotic and biotic disturbances, including fire and insect outbreaks (McCullough et al. 1998; Kurz et al. 2008). Although the direct effects of many of these factors have been evaluated, their interactions can be just as important. For example, insects may increase forest susceptibility to fire by rapidly killing many trees (e.g., Jenkins et al. 2008) and, conversely, fires provide weakened trees for colonisation by subcortical insects and pathogens (e.g., Six and Skov 2009), producing cascading and unpredictable changes in forest ecosystems. Further, biotic interactions, such as competition or predation, may be mediated by abiotic disturbances such as fire, drought, or flooding (e.g., Elderd 2006). This is especially noteworthy for



ecologically important species whose populations are influenced by interactions with natural enemies and competitors.

Bark beetle (Coleoptera: Curculionidae: Scolytinae) disturbance is an important biotic factor regulating forest ecosystems, affecting forest structure and tree species composition (Kurz et al. 2008; Bentz et al. 2010). *Dendroctonus ponderosae* Hopkins (mountain pine beetle) can cause extensive tree mortality during periodic outbreaks (Safranyik et al. 2010); for example, during the current outbreak, 50% of commercial *Pinus contorta* (lodgepole pine) has been killed in British Columbia, Canada during the last decade (Natural Resources Canada 2014). Prescribed fires have recently been introduced to western Canada to reduce pine forest susceptibility to *D. ponderosae* by breaking up even-aged stands. Thus, understanding the effects of fire on *D. ponderosae* populations is extremely important to forest management. In a recent study, I found that although *D. ponderosae* always attacked proportionally more trees in burned than in non-burned *P. contorta* stands, the rate of colonisation declined over 3 years after a pulse in the year of the fire (Chapter 2 of this thesis). Since *D. ponderosae* is influenced by a diverse community of subcortical insects at low-density populations (Boone et al. 2008), this decline may be partly due to fire-mediated interactions with the subcortical community, members of which are attracted to burned areas (Tabacaru and Erbilgin 2015 and Chapter 3 of this thesis). Specifically, since *D. ponderosae* is a poor competitor (Rankin and Borden 1991; Safranyik and Carroll 2006), examining the responses of the bark and ambrosia beetle community to fire will aid in describing *D. ponderosae* colonisation trends and improve our understanding of low-density population dynamics of tree-killing bark beetles in North America.

Bark and ambrosia beetles can be attracted to fire-injured trees, which are most suitable to insects that require stressed or weakened hosts (Rasmussen et al. 1996; McHugh et al. 2003). These beetles are responsible for most post-fire mortality and,

although most species do not generally outbreak, there is evidence that even so-called secondary bark beetles can significantly increase after fire and cause extensive tree mortality (Amman and Ryan 1991; Santoro et al. 2001). North American forests provide habitats for a plethora of bark and ambrosia beetles. For example, western *P. contorta* forests can support ~30 known species (Safranyik et al. 2004a), which likely interact extensively through competition, facilitation, or indirectly via natural enemies, and these interactions may alter the beetles' population growth trajectories (Rankin and Borden 1991; Safranyik and Carroll 2006; Wallin et al. 2008). Additionally, bark and ambrosia beetle species differ significantly in their life histories, and possibly in their responses to disturbance (Kirkendall 1983). Thus, a whole-community approach is necessary to understanding the complex effects of fire. For example, although certain bark and ambrosia beetle species are attracted to fire-injured trees, we do not yet understand the temporal changes in the community in burned forest stands, a factor which may ultimately help to characterise differences in the long-term responses of these biotic agents to fire.

Therefore, I sought to characterise the bark and ambrosia beetle community in burned and non-burned *P. contorta* forests and to examine if a disturbance (fire) can mediate the regulation of a tree-killing bark beetle by intensifying competition. I approached this objective by asking three questions: 1) can fire increase the numbers of bark and ambrosia beetles, potentially to outbreak levels; (2) what is the pattern of bark and ambrosia beetle community progression into burned areas after fire; and (3) can bark and ambrosia beetles affect *D. ponderosae* colonisation of burned areas?

## 4.2 Materials and methods

### 4.2.1 Study sites and fire injury classes

I worked in three prescribed fire sites in mature *P. contorta* forests within the Alberta Rocky Mountains, all burned in spring 2009. The Mt. Nestor fire (115° 22'55.617" W, 50° 54'25.073" N; elevation of centre 1800 m) was the smallest (618 ha), and was used to improve habitat for grizzly bears (*Ursus arctos*), bighorn sheep (*Ovis canadensis*), and whitebark pine (*Pinus albicaulis*). Most of the fire occurred in areas with a 200–250 year fire cycle (Rogean et al. 2004). The Upper Saskatchewan fire (116° 37'2.310" W, 52° 1'17.964" N; elevation of centre 1400 m) was the largest (4,623 ha), and was used to reduce stand susceptibility to *D. ponderosae* and to restore natural fire regime vegetation types. The majority of this fire occurred in areas with a 100–150 year fire cycle, although some areas had 201–250 and 251–300 year fire cycles (Rogean et al. 2004). The Ya Ha Tinda fire (115° 36'35.079" W, 51° 44'07.784" N; elevation of centre 1700 m) was moderately sized (1,264 ha), and was primarily used to reduce stand susceptibility to *D. ponderosae*. It occurred in areas with a 64–98 year fire cycle (Rogean 2009). The fires were all of mixed-severity. All forests contained low-density populations of *D. ponderosae* and were separated by > 100 km.

I divided fire injury into three classes: non-burned, low, and moderate. These were defined using Parks Canada burn severity classifications, which are based on US Geological Survey techniques (Soverel et al. 2010). I used ArcGIS 9.2 (ESRI, Redlands, CA, U.S.A.) to randomly locate at least 15 10 × 10-m plots, placed a minimum of 200 m apart, in each fire injury class at each site. After plot establishment, I visually estimated the bole (trunk) char of each tree and averaged these per plot as a general measure of fire injury. Parks Canada's non-burned, low, and moderate classes generally corresponded to 0% bole char, 1%–15% bole char (mean for all sites 10.86%), and ≥ 16%

bole char (mean 31.42%), respectively. Rarely, I found areas of low fire injury in Parks Canada's moderate class and vice-versa; I categorised plots in these areas according to bole char.

#### **4.2.2 *Dendroctonus ponderosae* attack and beetle collection**

I quantified annual *D. ponderosae* attacks per plot for 4 consecutive years (2009–2012), using the characteristic pitch tubes (exuded sap) of *D. ponderosae* and frass (insect faeces and boring dust) to determine attack. I did not assess attacks below 1 m on the trunk to avoid including lower-stem-colonising bark beetles. Trees were generally not killed by *D. ponderosae*.

To survey a wide variety of bark and ambrosia beetle species, I used three types of passive traps (i.e., without attractants): emergence (Fig. 3.1), landing (Fig. 3.2), and flight intercept (Fig. 3.3). Passive traps are necessary when the goal is to determine abundance and species richness without artificially attracting individuals from areas outside the study site. For 3 consecutive years (2010–2012) at each site, I placed 3–5 traps of each type in each of the three fire injury classes in late May, and collected traps once at the end of the season (late August). For each emergence trap, I wrapped a 1 × 2-m fine mesh cloth (< 0.5 mm), with a 2-m cloth funnel, around a tree trunk between heights of 1 and 2 m. A 105-mL urine sample cup, whose lid was drilled to leave only the frame, was filled with 10 mL of 50% propylene glycol solution diluted with water, and attached to the bottom of each cloth funnel using a standard pipe clamp. Lids were used because cups were too flimsy to hold the pipe clamps. During collection, cups were removed and sealed with non-drilled lids. For landing traps, I cut the bottom from 2-L soda bottles, and cut the bottles in half length-wise. To ensure easy attachment and detachment of collection cups, I glued drilled threaded lids to the inverted bottle tops, which became funnels. To each lid, I attached a 105-mL

plastic sample cup filled with 10 mL of 50% propylene glycol solution, diluted with water. I then attached traps to tree trunks at breast height (1.3 m). During collection, cups were removed as for emergence traps. Finally, I hung flight intercept panel traps (Advanced Pheromone Technologies, Marylhurst, OR, U.S.A.) between two trees at least 1 m off the ground using rope. Collection cups were filled with 50 mL of 50% propylene glycol solution, diluted with water. For collection, cups were removed and all liquid was poured into 1-L Nalgene bottles (Thermo Fisher Scientific Inc., Waltham, MA, U.S.A.). Flight intercept traps were left in the same locations year to year, landing traps were always placed on live trees, and were moved only if trees had died over the winter, and emergence traps were always moved to new trees within the same plot to avoid excluding insects. Following field collection, I sorted, identified, and stored bark beetles in a 70% ethanol solution. I identified one group of beetles to near the genus *Pityophthorus* using the key in Bright (1976), but could not identify them further. I will be referring to this group as *Pityophthorus* hereafter.

I grouped bark and ambrosia beetle species, or genera when species could not be identified, into four feeding guilds according to Wood (1982): lower stem/lateral root-colonising bark beetles (hereafter lower-stem bark beetles), main-stem bark beetles, upper stem/branch/twig-colonising bark beetles (hereafter upper-stem bark beetles), and ambrosia beetles. Where species' preferences were unavailable, I used the general biology of genera. Lower-stem bark beetles generally attack trees below 1 m on the trunk and can also be found in stumps and roots. Main-stem bark beetles generally attack trees between 1 and 2 m on the trunk. Upper-stem bark beetles attack the trunk past the beginning of the canopy, and can also be found in branches or twigs, sometimes preferentially. Ambrosia beetles generally colonise the xylem (not the phloem as bark beetles do) and cultivate fungi that digest it, which they then feed on. I divided beetles into these groups because fire likely affects trees, and thus beetles feeding on those

trees, differently at different heights. For example, ground fire may affect roots and lower boles, but not twigs and branches in the canopy.

### 4.2.3 Statistical analyses

All statistical analyses were performed using R v. 3.0.2 (R Development Core Team 2013). All bark and ambrosia beetle abundances were standardised to account for differences in the numbers of trapping days (Table 4.1). Although *D. ponderosae* abundances are included in Table 4.1, I did not use them in any statistical analysis to avoid correlation with *D. ponderosae* attacks and to allow discussion of community effects on this species.

To visualise the effects of fire injury class and year on the bark and ambrosia beetle communities at each site, I used Nonmetric Multidimensional Scaling (NMDS; *ecodist* package in R), an ordination method suited to community data with many zeroes (McCune and Grace 2002). I used the Bray-Curtis dissimilarity as a distance measure, with which distances between samples were ranked. These were then represented in a low-dimensional configuration which minimises stress, a measure of how well the configuration displays more similar points closer together. I performed a separate analysis for each site for a total of three NMDS analyses. Furthermore, I used Permutational Multivariate Analyses of Variance (PerMANOVA; *ecodist* package in R) to test the responses of bark beetle genera at each site to fire injury class and year, as well as any interactions between them. PerMANOVA can test non-normal community data, using distances to compare groups by calculating a test statistic that represents the ratio of distances between groups to distances within groups. I again used the Bray-Curtis dissimilarity for distance calculations. I also used PerMANOVAs to test for differences in the bark and ambrosia beetle community at each site between areas with and without *D. ponderosae*, and among years, and any interactions between them. I checked all data

Table 4.1: Standardised mean abundance (per trap day) of bark and ambrosia beetles (Curculionidae: Scolytinae), divided among feeding guilds, fire injury classes (non-burned and burned), sites, and years. 2010 refers to 1 year after fire, 2011 refers to 2 after fire, and 2012 refers to 3 years after fire. MN = Mt. Nestor, US = Upper Saskatchewan, YHT = Ya Ha Tinda Ranch, N = non-burned, B = burned. Main stem = main-stem beetles, Upper stem = upper-stem/branch/twig beetles, Lower stem = lower-stem/root/stump beetles, Ambrosia = ambrosia beetles. Empty cells represent zero values. Zeroes represent non-zero values that have been rounded to zero.

Species	2010									2011									2012									
	MN			US			YHT			MN			US			YHT			MN			US			YHT			
	N	B		N	B		N	B		N	B		N	B		N	B		N	B		N	B		N	B		
<b>Main stem</b>																												
<i>Dendroctonus ponderosae</i>																												
<i>Dendroctonus rufipennis</i>	0.002	0.002		0.002	0.002		0.001																					
<i>Dendroctonus</i> spp.																												
<i>Ips perturbatus</i>																												
<i>Ips pini</i>	0.002	0.003		0.007	0.007		0.001	0.018																				
<i>Ips</i> spp.																												
<i>Pityokteines minutus</i>																												
<i>Polygraphus rufipennis</i>																												
<i>Scolytus</i> spp.				0.002			0.001																					
<i>Xylechinus montanus</i>				0.002			0.001																					
<b>Upper stem</b>																												
<i>Ips latidens</i>	0.005	0.003		0.007	0.007		0.003	0.003																				
<i>Pityogenes</i> spp.		0.059					0.002																					
near <i>Pityophthorus</i>		0.003		0.002	0.002																							
<i>Pseudopityophthorus</i> spp.																												
<i>Scolytus piceae</i>				0.002			0.001																					
<b>Lower stem</b>																												
<i>Dendroctonus murrayanae</i>																												
<i>Dendroctonus valens</i>	0.007	0.007		0.010	0.010		0.001	0.002																				
<i>Dryocoetes affaber</i>																												
<i>Dryocoetes autographus</i>																												
<i>Dryocoetes</i> spp.																												
<i>Hylastes gracilis</i>	0.002	0.003		0.004	0.004		0.000	0.000																				
<i>Hylastes longicollis</i>	0.002																											
<i>Hylastes nigricollis</i>																												
<i>Hylastes porosus</i>		0.002		0.002	0.002		0.000	0.001																				
<i>Hylastes ruber</i>																												
<i>Hylastes</i> spp.																												
<i>Hylurgops porosus</i>	0.002	0.011		0.001	0.001		0.001	0.003																				
<i>Hylurgops rugipennis</i>				0.001	0.001		0.001	0.001																				
<i>Hylurgops</i> spp.																												
<i>Ips emarginatus</i>																												
<i>Orthotomicus caelatus</i>								0.001																				
<i>Pseudips mexicanus</i>																												
<i>Scierus annexens</i>	0.002	0.002																										
<i>Sclerius pubescens</i>																												
<b>Ambrosia</b>																												
<i>Gnathotrichus</i> spp.																												
<i>Trypodendron</i> spp.																												
<i>Xyleborus xylographus</i>	0.002	0.002		0.001	0.001		0.001	0.002																				

for multivariate homogeneity of group dispersions before implementing PerMANOVAs (*vegan* package in R).

Next, I used a mixed-effects ANOVA (*nlme* package in R), with site as a random effect, to determine the effects of fire injury class and year, and any interaction between them, on overall bark and ambrosia beetle abundance, which included all species and genera. As well, I used permutational ANOVAs (*lmPerm* package in R) to determine any effects of fire injury class, year, and/or *D. ponderosae* presence on individual feeding guild groups. This allowed me to infer which groups were most influential to community results. Finally, I used permutational ANOVAs to test the effects of fire injury class and year on one (abundant) representative species/genus from each feeding guild at one site: *Ips latidens* (upper-stem bark beetles; Upper Saskatchewan), *Ips pini* (main-stem bark beetles; Upper Saskatchewan), *Dendroctonus murrayanae* (lower-stem bark beetles; the Ya Ha Tinda Ranch), and *Trypodendron* spp. (ambrosia beetles; Mt. Nestor). Sites and representatives were chosen based on abundance and trend, since our aim was to show that some species/genera can increase over time.

In this chapter, I considered significance at both  $\alpha = 0.05$  and  $\alpha = 0.1$  because, although the probability of Type I error increases with increasing values of  $\alpha$ , prescribed fire is a complicated management technique affecting many aspects of forest ecosystems, and the consequences of not considering bark beetle responses when they occur are arguably greater than those of erroneously concluding that they exist.

## 4.3 Results

### 4.3.1 Responses of the bark and ambrosia beetle community to fire

Because bark and ambrosia beetles did not differentiate between the low and moderate fire injury classes, I combined the two, resulting in two classes: burned and



non-burned. Species that were found exclusively in burned stands include (in order of abundance, then alphabetised) *Dryocoetes autographus*, *Dryocoetes affaber*, *Pityokteines minutus*, *Orthotomicus caelatus*, *Dendroctonus valens*, *Ips perturbatus*, *Ips emarginatus*, *Pseudips mexicanus*, *Scierus pubescens*, *Xyleborus xylographus*, and *Hylastes nigrinus*. No species were found exclusively in non-burned stands.

Overall, according to NMDS analyses, upper-stem bark beetles were consistently associated with burned areas, and although there was no clear pattern for other feeding groups, all were often associated with burned areas (Figs. 4.1–4.3). At Mt. Nestor (Fig. 4.1; two axes, stress < 0.3), upper-stem bark beetles were associated with burned areas, while main- and lower-stem bark beetles had no clear pattern, although they also showed loose associations with burned areas. Ambrosia beetles at Mt. Nestor were associated with non-burned areas. Furthermore, upper-stem bark beetles were associated with 1 year after fire, while main- and lower-stem bark beetles also tended toward 1 year after fire, but had weaker associations. Ambrosia beetles were associated with 2 and 3 years after fire. At Upper Saskatchewan (Fig. 4.2; stress 0.24), all three groups were associated with burned stands and 2 and 3 years after fire. Similarly, at the Ya Ha Tinda Ranch (Fig. 4.3; two axes, stress < 0.3), all groups were associated with burned areas and 2 and 3 years after fire.

With respect to fire injury and year following fire, PerMANOVA results showed that the bark and ambrosia beetle community differed between fire injury classes at all three sites (Table 4.2). The community differed among years at Upper Saskatchewan and the Ya Ha Tinda Ranch, and there were no interactions between fire injury class and year (Table 4.2). The community differences between classes were mainly driven by upper-stem bark beetles ( $df = 1, 59, P < 0.001$ ) and ambrosia beetles ( $df = 1, 59, P < 0.01$ ) at Mt. Nestor, by upper-stem bark beetles at Upper Saskatchewan ( $df = 1, 98, P = 0.053$ ), and by main-stem bark beetles at the Ya Ha Tinda Ranch ( $df = 1, 79,$

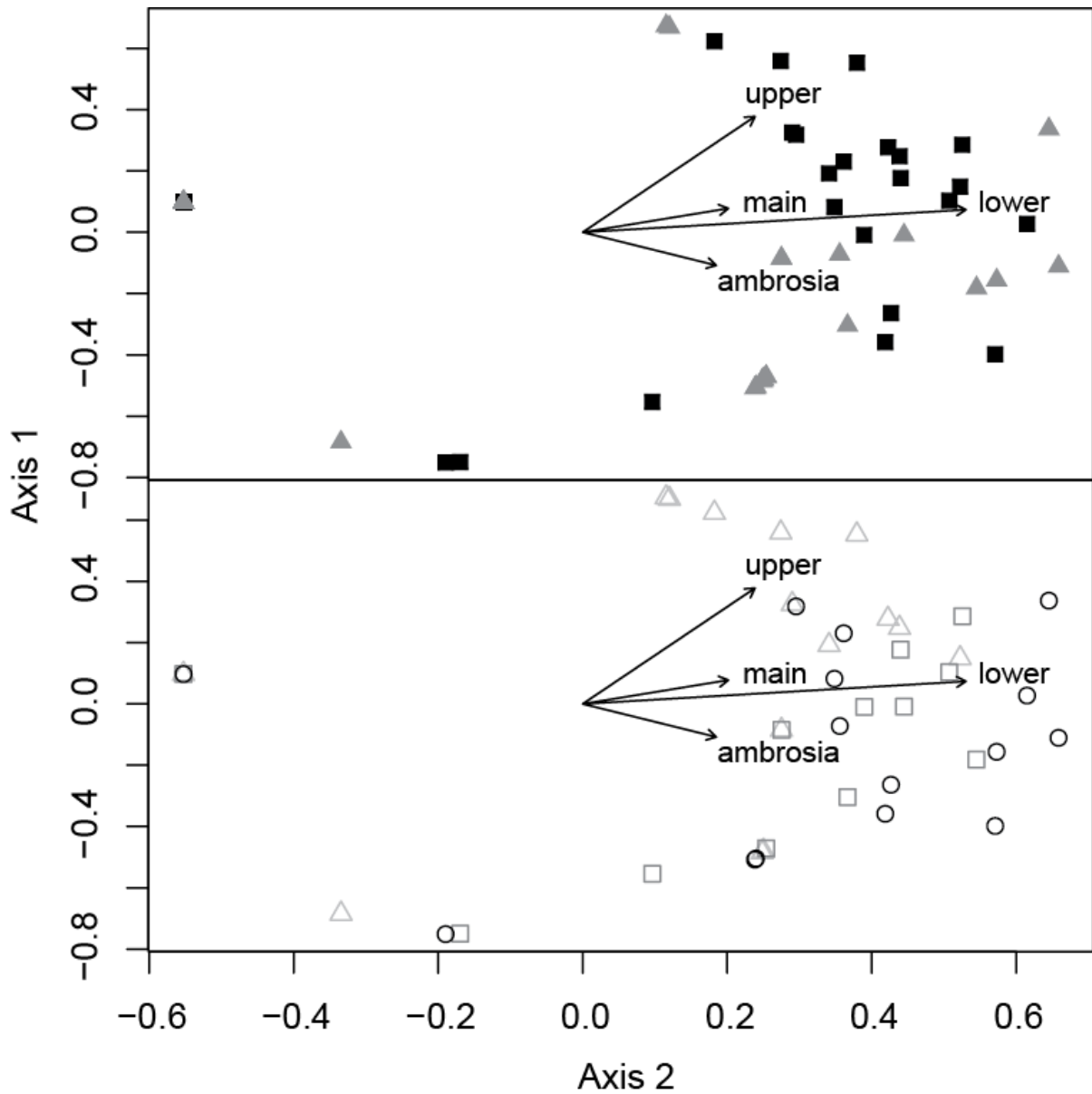


Figure 4.1: Visualisation of the effects of a) fire injury (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on bark beetle feeding guilds at Mt. Nestor, using Nonmetric Multidimensional Scaling (NMDS). a) Black filled squares represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open light grey triangles represent traps collected 1 year after fire, open medium grey squares represent traps collected 2 years after fire, and open black circles represent traps collected 3 years after fire. lower = lower stem/stump/root bark beetles, main = main-stem bark beetles, upper = upper stem/branch/twig bark beetles, ambrosia = ambrosia beetles.

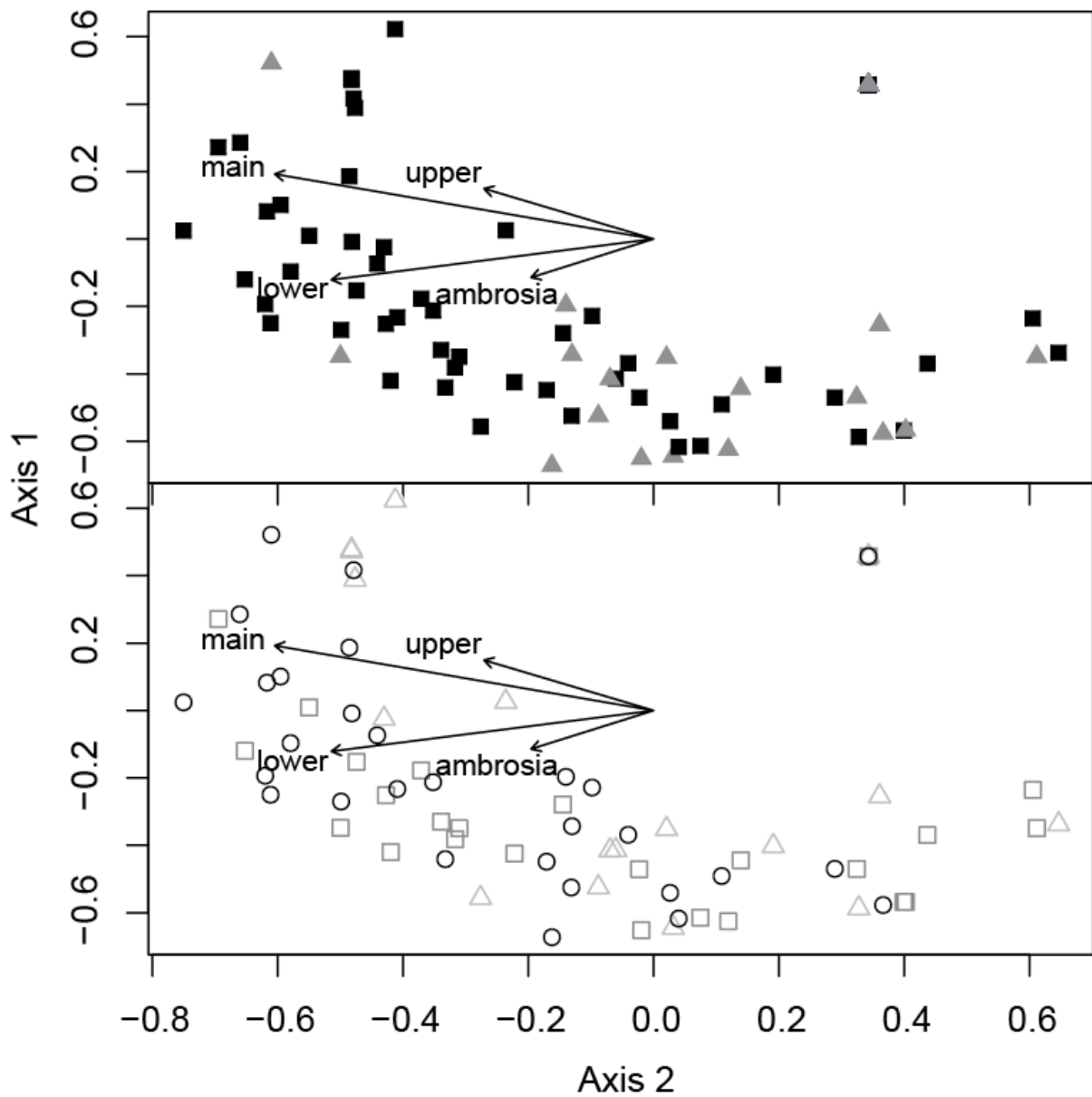


Figure 4.2: Visualisation of the effects of a) fire injury (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on bark beetle feeding guilds at Upper Saskatchewan, using Nonmetric Multidimensional Scaling (NMDS). a) Black filled squares represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open light grey triangles represent traps collected 1 year after fire, open medium grey squares represent traps collected 2 years after fire, and open black circles represent traps collected 3 years after fire. lower = lower stem/stump/root bark beetles, main = main-stem bark beetles, upper = upper stem/branch/twig bark beetles, ambrosia = ambrosia beetles.

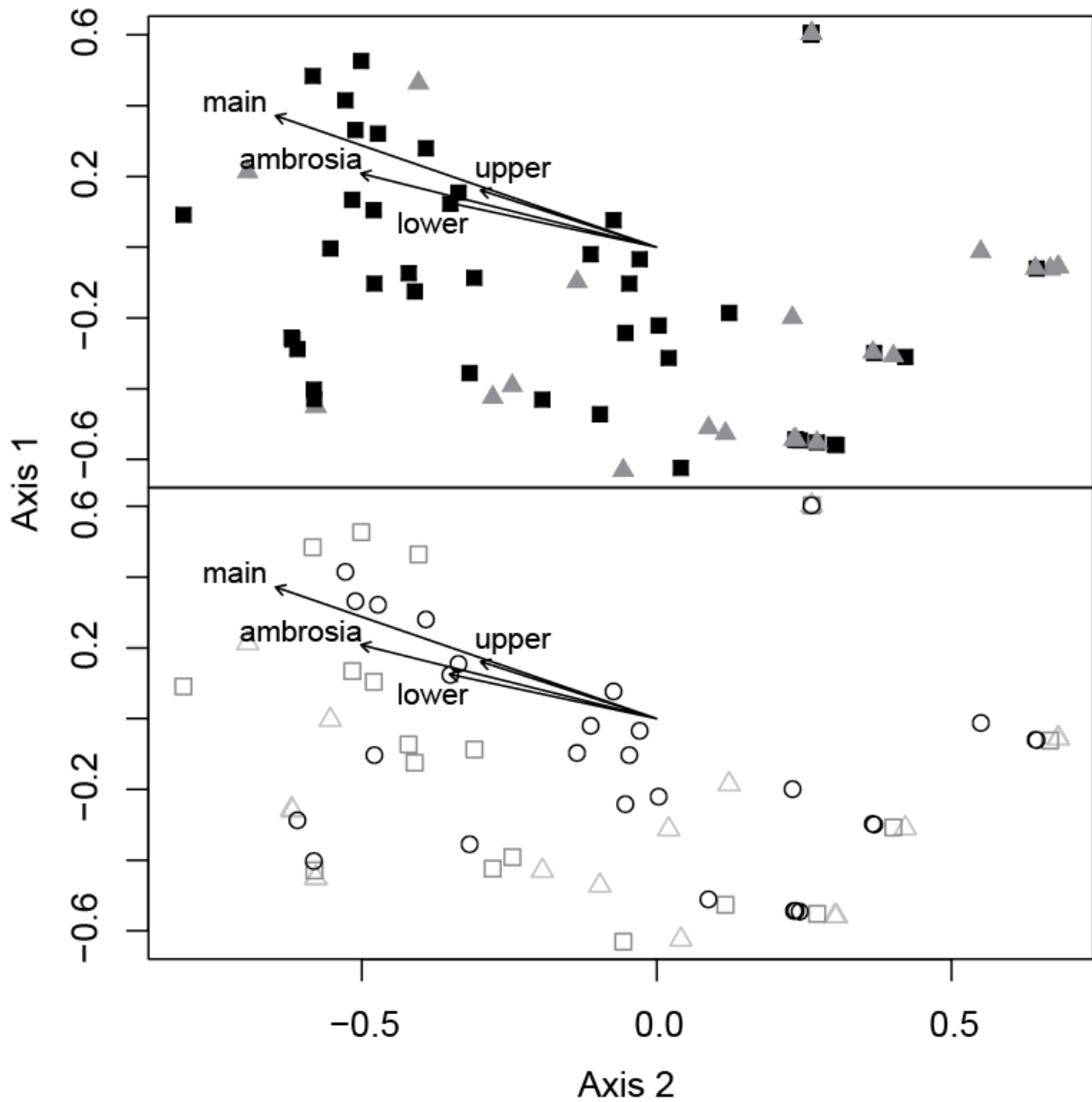


Figure 4.3: Visualisation of the effects of a) fire injury (burned and non-burned) and b) year after fire (2010–2012 or years 1–3) on bark beetle feeding guilds at the Ya Ha Tinda ranch, using Nonmetric Multidimensional Scaling (NMDS). a) Black filled squares represent traps at burned plots and grey filled triangles represent traps at non-burned plots. b) Open light grey triangles represent traps collected 1 year after fire, open medium grey squares represent traps collected 2 years after fire, and open black circles represent traps collected 3 years after fire. lower = lower stem/stump/root bark beetles, main = main-stem bark beetles, upper = upper stem/branch/twig bark beetles, ambrosia = ambrosia beetles.

Table 4.2: Results of three Multivariate Permutational Analyses of Variance (PerMANOVA), depicting the effects of year after fire (1, 2, or 3) and fire injury class (burned or non-burned) on the bark and ambrosia beetle (Curculionidae: Scolytinae) community at each of three study sites: Mt. Nestor, Upper Saskatchewan, and the Ya Ha Tinda Ranch. \* denotes significant effects at  $\alpha = 0.1$ , \*\* denotes significant effects at  $\alpha = 0.05$ .

Site	Variable	DF	F	P
Mt. Nestor	Year	2	1.51	0.16
	Fire injury	1	3.07	0.03**
	Year × Fire injury	2	0.97	0.44
Upper Saskatchewan	Year	2	5.48	0.004**
	Fire injury	1	2.08	0.091*
	Year × Fire injury	2	1.86	0.10
Ya Ha Tinda Ranch	Year	2	2.80	0.024**
	Fire injury	1	2.60	0.031**
	Year × Fire injury	2	1.59	0.16

$P = 0.062$ ). Community differences among years were driven by main- (df = 1, 98,  $P < 0.05$ ) and upper- (df = 1, 98,  $P < 0.01$ ) stem bark beetles at Upper Saskatchewan, and by upper-stem bark beetles at the Ya Ha Tinda Ranch (df = 1, 79,  $P < 0.05$ ).

With respect to *D. ponderosae* presence and year following fire, PerMANOVA results show that the bark and ambrosia beetle community differed between areas with and without *D. ponderosae* at Mt. Nestor and the Ya Ha Tinda Ranch (Table 4.3). I also found an interaction between year after fire and *D. ponderosae* presence at Upper Saskatchewan (Table 4.3). The community differences between areas with and without *D. ponderosae* were mainly driven by upper-stem bark beetles at Mt. Nestor (df = 1, 58,  $P < 0.01$ ) and by upper- (df = 1, 79,  $P < 0.05$ ) and lower- (df = 1, 79,  $P < 0.001$ ) stem bark beetles at the Ya Ha Tinda Ranch. Finally, the interaction at Upper Saskatchewan was driven by lower-stem bark beetles (df = 2, 96,  $P = 0.079$ ).

Table 4.3: Results of three Multivariate Permutational Analyses of Variance (PerMAN-OVA), depicting the effects of year after fire (1, 2, or 3) and *D. ponderosae* (presence or absence) on the bark and ambrosia beetle (Curculionidae: Scolytinae) community at each of three study sites: Mt. Nestor, Upper Saskatchewan, and the Ya Ha Tinda Ranch. \* denotes significant effects at  $\alpha = 0.1$ , \*\* denotes significant effects at  $\alpha = 0.05$ .

Site	Variable	DF	F	P
Mt. Nestor	Year	2	1.55	0.16
	<i>D. ponderosae</i>	1	2.54	0.051*
	Year $\times$ <i>D. ponderosae</i>	2	1.36	0.23
Upper Saskatchewan	Year	2	3.64	0.002**
	<i>D. ponderosae</i>	1	1.53	0.16
	Year $\times$ <i>D. ponderosae</i>	2	2.17	0.037**
Ya Ha Tinda Ranch	Year	2	3.18	0.014**
	<i>D. ponderosae</i>	1	2.06	0.079*
	Year $\times$ <i>D. ponderosae</i>	2	1.34	0.22

### 4.3.2 Post-fire bark and ambrosia beetle abundance

Using a mixed-effects ANOVA, I found that overall bark and ambrosia beetle abundances differed among years after fire ( $F_{2,242} = 3.74$ ,  $P < 0.05$ ), but did not differ between fire injury classes (Fig. 4.4). Specifically, I found significantly more beetles in 2012 than in 2010 ( $P < 0.05$ ; Fig. 4.4). Standardised abundances for individual feeding groups at each site are displayed in Figures 4.5–4.7. Additionally, I found that representatives from upper-, main-, and lower-stem bark beetle groups all increased over time (Fig. 4.8). Specifically, *I. latidens*, an upper-stem bark beetle, *I. pini*, a main-stem bark beetle, and *D. murrayanae*, a lower-stem bark beetle, increased from 2010 to 2012 (*I. latidens*:  $df = 2, 98$ ,  $P = 0.087$ ; *I. pini*:  $df = 2, 98$ ,  $P = 0.066$ ; *D. murrayanae*:  $df = 2, 79$ ,  $P < 0.01$ ). *Trypodendron* spp. only differed in abundance between fire injury classes ( $df = 1, 59$ ,  $P < 0.01$ ).

I characterised the progression of beetle movement into burned areas according to the beetles' feeding groups. In general, upper-stem bark beetles were the most abundant 1 year after fire, main-stem bark beetles and ambrosia beetles were the most

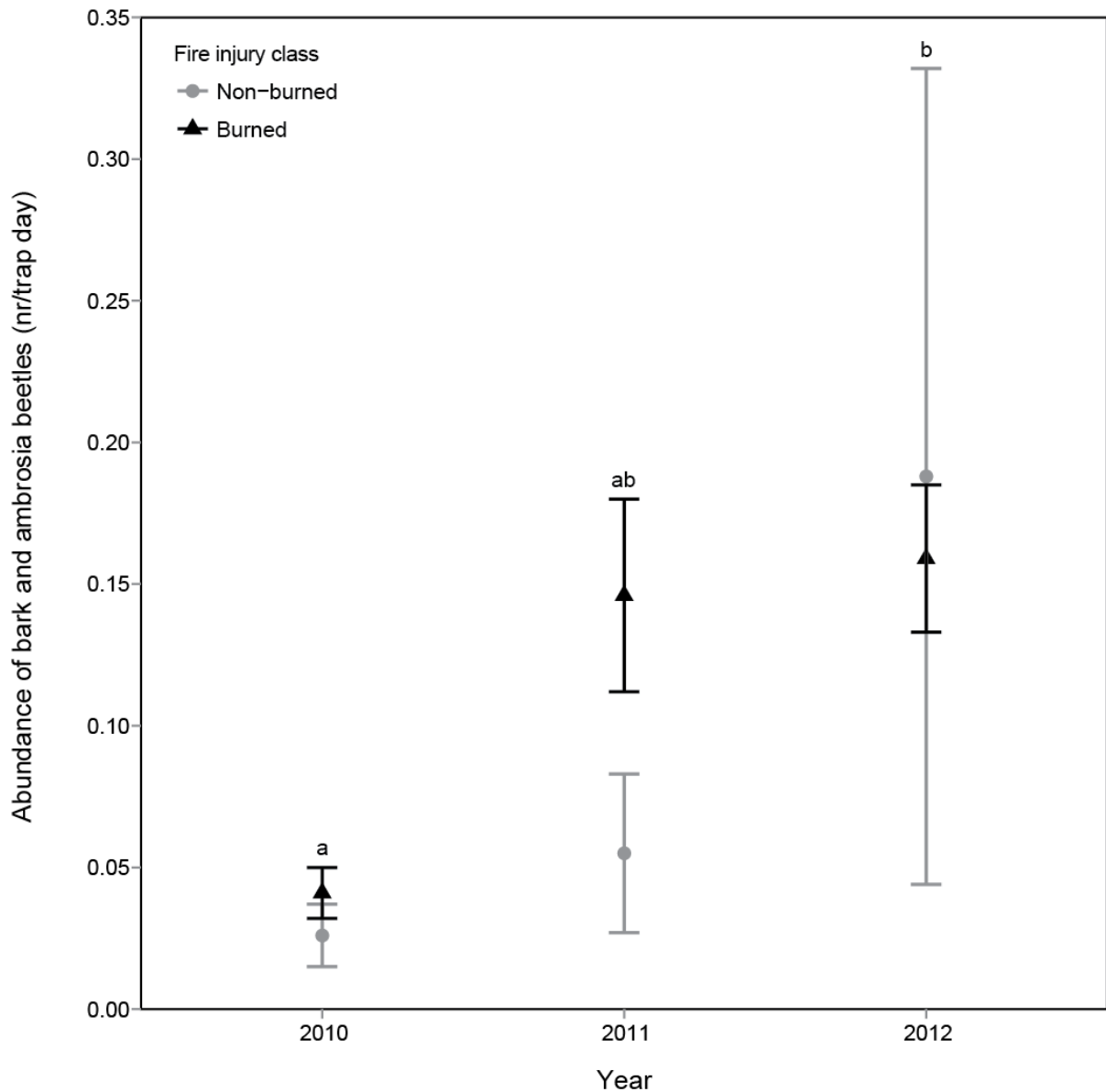


Figure 4.4: Standardised mean abundance (per trap day)  $\pm$  SE of bark and ambrosia beetles (Curculionidae: Scolytinae), divided between fire injury classes (non-burned and burned) and years. 2010 refers to 1 year after fire, 2011 refers to 2 years after fire, and 2012 refers to 3 years after fire. Different letters represent significant differences among years, after a mixed-effects ANOVA. There were no significant differences between fire injury classes.

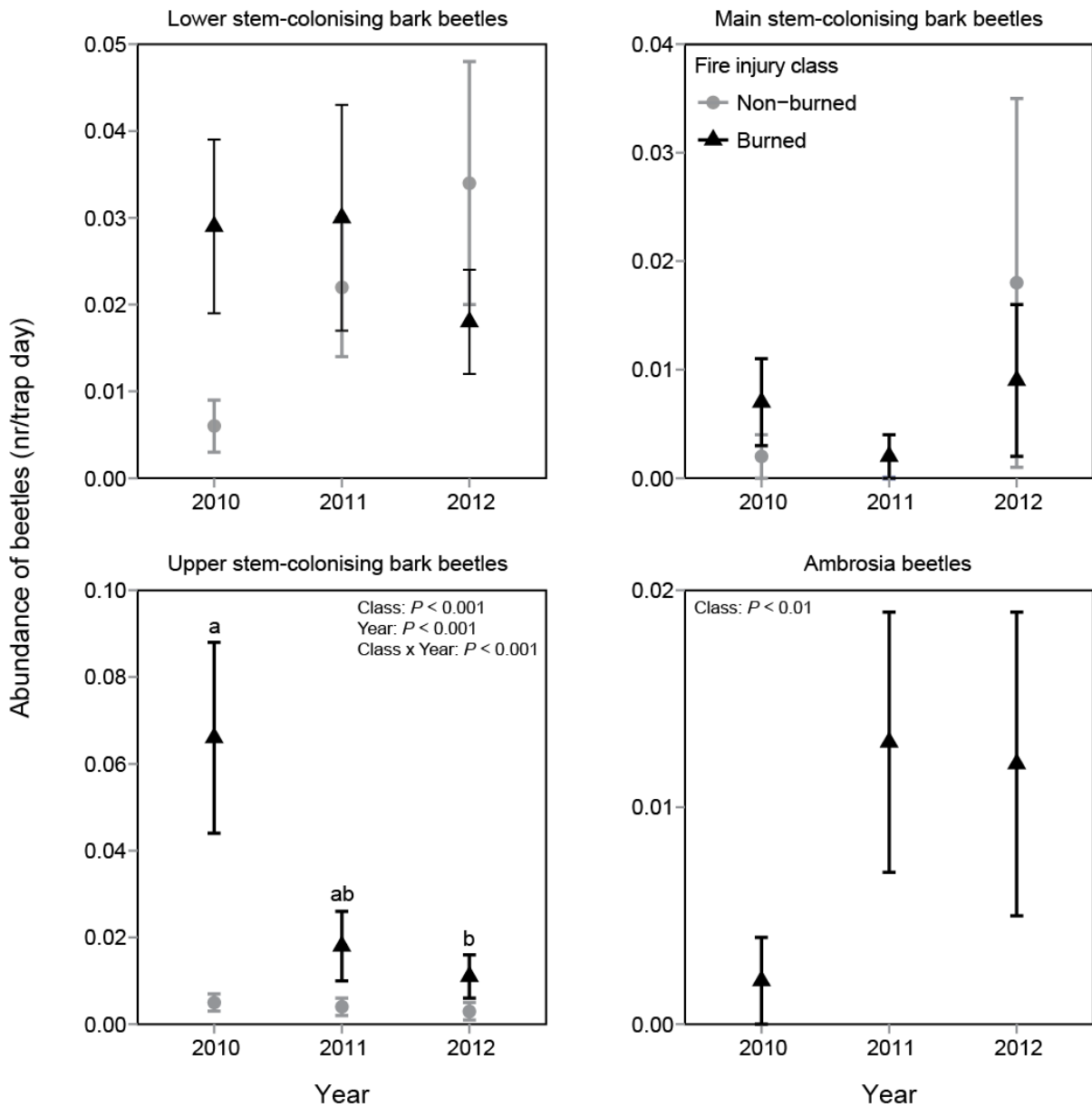


Figure 4.5: Standardised mean abundance (per trap day)  $\pm$  SE of bark and ambrosia beetles (Curculionidae: Scolytinae) at Mt. Nestor, divided between fire injury classes (non-burned and burned) and years. 2010 refers to 1 year after fire, 2011 refers to 2 years after fire, and 2012 refers to 3 years after fire. Zero values do not appear in graphs. Only statistically significant (at  $\alpha = 0.05$  or  $0.1$ ) main effects or interactions appear in graphs. Different letters indicate significant differences among years. Class = fire injury class.



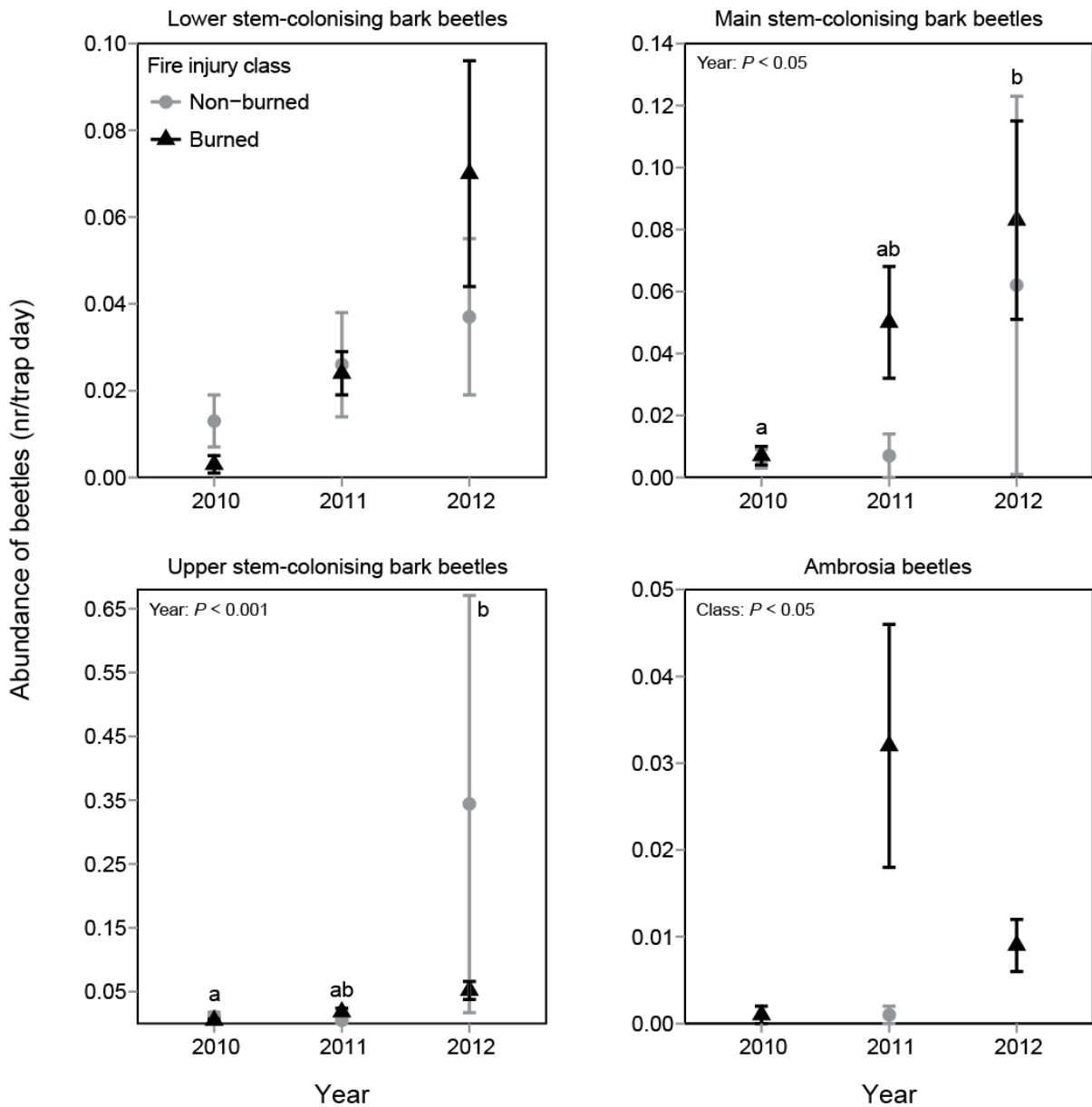


Figure 4.6: Standardised mean abundance (per trap day)  $\pm$  SE of bark and ambrosia beetles (Curculionidae: Scolytinae) at Upper Saskatchewan, divided between fire injury classes (non-burned and burned) and years. 2010 refers to 1 year after fire, 2011 refers to 2 years after fire, and 2012 refers to 3 years after fire. Zero values do not appear in graphs. Only statistically significant (at  $\alpha = 0.05$  or  $0.1$ ) main effects or interactions appear in graphs. Different letters indicate significant differences among years. Class = fire injury class.

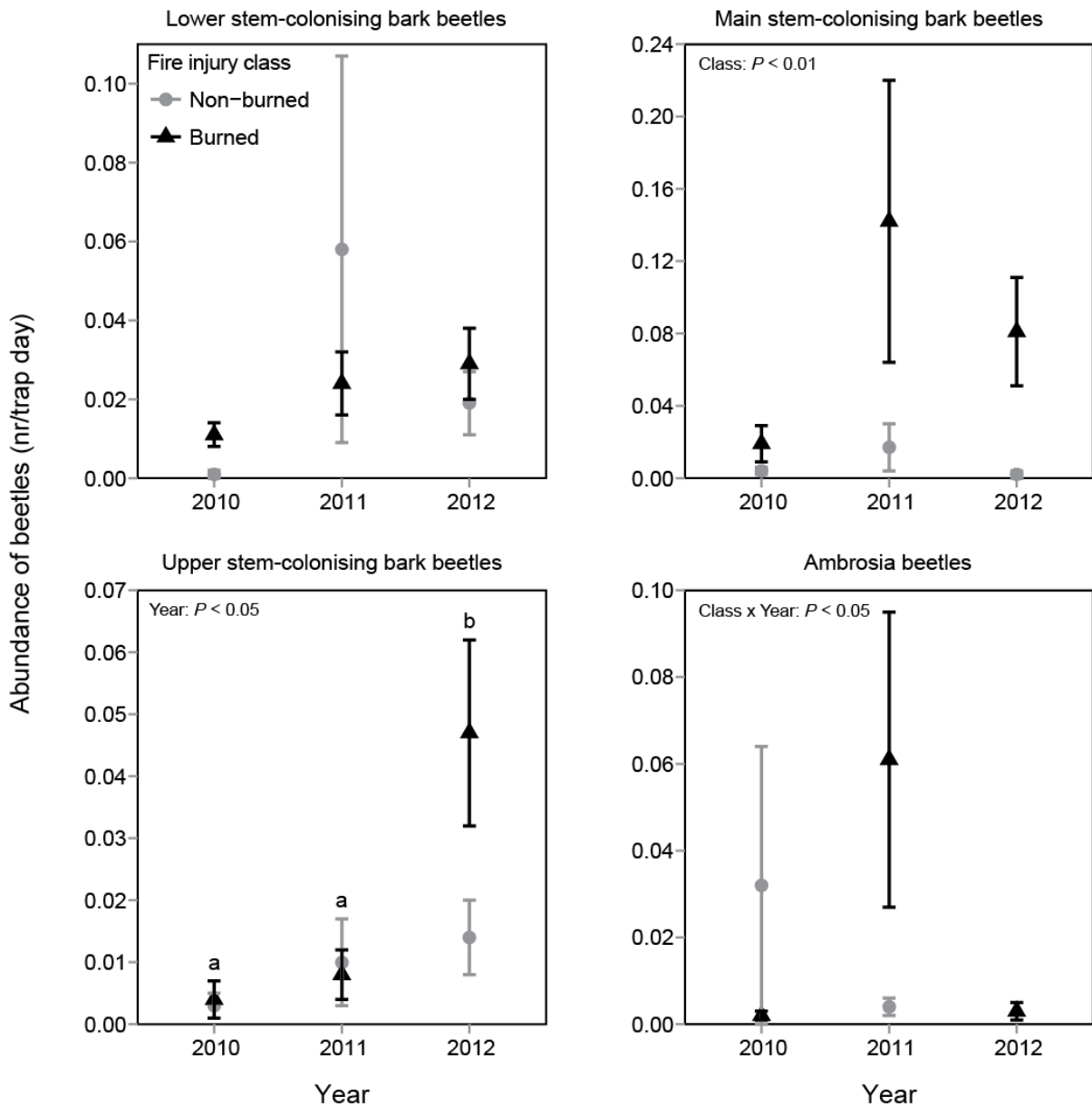


Figure 4.7: Standardised mean abundance (per trap day)  $\pm$  SE of bark and ambrosia beetles (Curculionidae: Scolytinae) at the Ya Ha Tinda Ranch, divided between fire injury classes (non-burned and burned) and years. 2010 refers to 1 year after fire, 2011 refers to 2 years after fire, and 2012 refers to 3 years after fire. Zero values do not appear in graphs. Only statistically significant (at  $\alpha = 0.05$  or 0.1) main effects or interactions appear in graphs. Different letters indicate significant differences among years. Class = fire injury class.

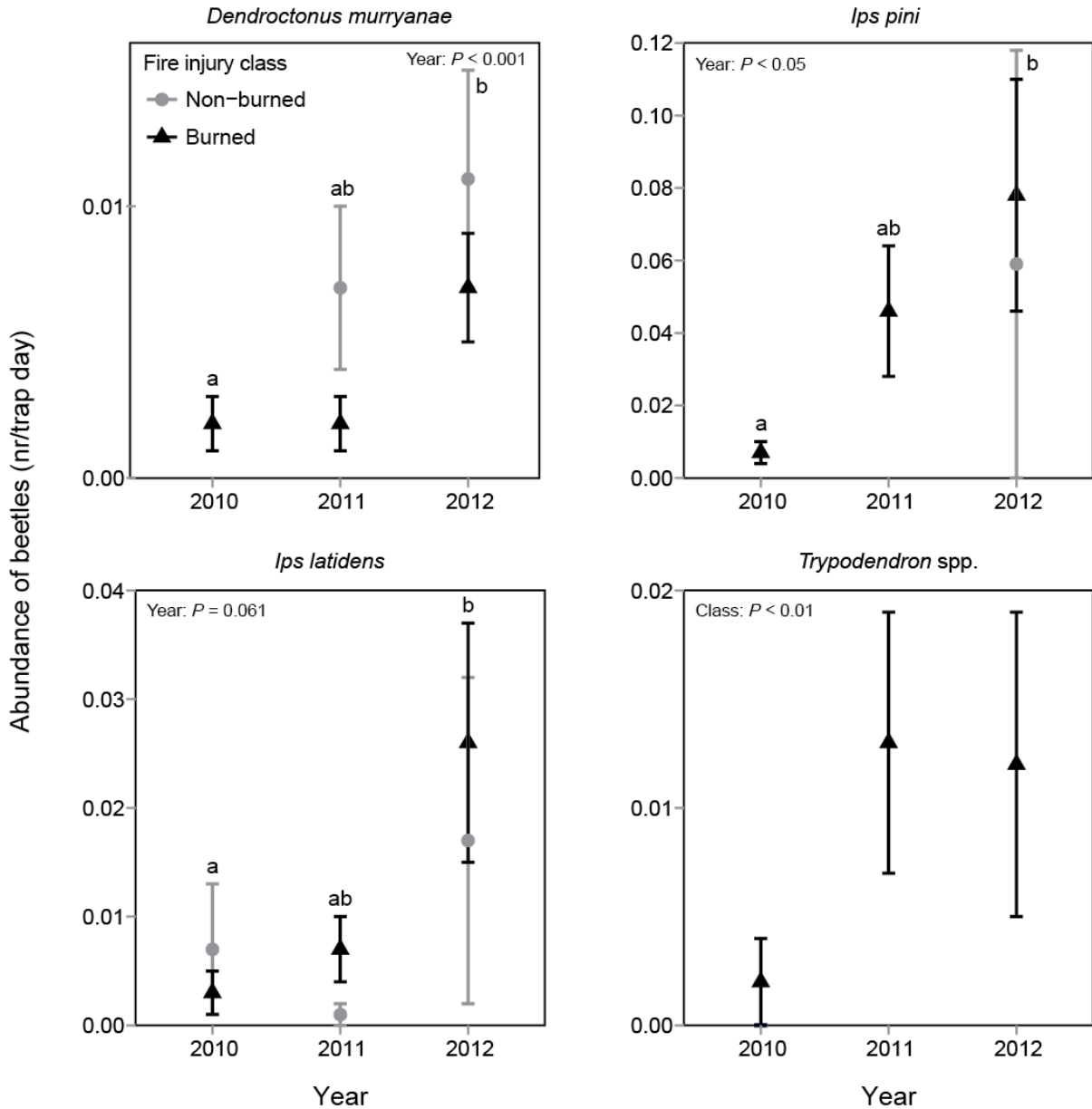


Figure 4.8: Standardised mean abundance (per trap day)  $\pm$  SE of bark and ambrosia beetle species (Curculionidae: Scolytinae) divided between fire injury classes (non-burned and burned) and years. *Dendroctonus murrayanae* (at the Ya Ha Tinda Ranch) represents lower-stem colonising bark beetles, *Ips pini* (at Upper Saskatchewan) represents main-stem colonising bark beetles, *Ips latidens* (at Upper Saskatchewan) represents upper-stem colonising bark beetles, and *Trypodendron* spp. (at Mt. Nestor) represents ambrosia beetles. 2010 refers to 1 year after fire, 2011 refers to 2 years after fire, and 2012 refers to 3 years after fire. Zero values do not appear in graphs. Only statistically significant (at  $\alpha = 0.05$  or 0.1) main effects or interactions appear in graphs. Different letters indicate significant differences among years.

abundant 2 years after fire, and lower- and main-stem bark beetles were the most abundant 3 years after fire. At Mt. Nestor, I found relatively high abundances of upper- and lower-stem bark beetles in burned areas 1 year after fire. Ambrosia beetles increased 2 and 3 years after fire, while main-stem bark beetles remained at relatively low and constant abundances over time. At Upper Saskatchewan, all groups were at low abundances 1 year after fire. Lower- and main-stem bark beetles and ambrosia beetles increased 2 years after fire. Lower- and main-stem bark beetles continued to increase 3 years after fire, while upper-stem bark beetles also began to increase. At the Ya Ha Tinda Ranch, all groups were again at low abundances in burned areas 1 year after fire. Lower- and main-stem bark beetles and ambrosia beetles increased 2 years after fire. Lower-stem bark beetles continued at a constant abundance 3 years after fire, while upper-stem bark beetles increased.

## **4.4 Discussion**

Bark and ambrosia beetle communities were affected by both fire and year after fire, wherein I observed generally more beetles in burned stands, and some species became more abundant over time. However, both feeding group and site strongly affected these responses. This study provides the first field evidence that *D. ponderosae* at low densities experiences increased competition from members of the subcortical community shortly after prescribed fire.

### **4.4.1 Can fire increase bark and ambrosia beetle abundances?**

In general, all functional groups of beetles increased in number over time, at least until 2 years after fire, in both burned and non-burned *P. contorta* stands. Broadly speaking, the changes in overall abundance in non-burned stands were similar to those

in burned stands, but lagged by approximately 1 year, i.e., beetles increased more rapidly in burned stands. Additionally, I found that some species increased over time in both types of stands, providing compelling evidence of potential outbreaks originating in post-fire pine stands. The idea that bark beetles can build up their populations in weakened trees after fire and subsequently attack healthy adjacent stands has been previously proposed (e.g., Furniss 1965; Amman and Ryan 1991; Rasmussen et al. 1996; McHugh et al. 2003), but few studies have examined attacks in non-burned stands (but see Amman and Ryan 1991; Rasmussen et al. 1996). Here, I found that *I. pini*, a main-stem bark beetle, increased over time in both burned and adjacent non-burned stands. Similarly, *I. latidens* and *D. murrayanae*, upper- and lower-stem bark beetles, respectively, also increased over time regardless of fire injury class. Both *I. latidens* (Miller et al. 1986) and *D. murrayanae* (Furniss and Kegley 2008) are attracted to stressed host trees, although our study is the first to demonstrate their increased abundance in response to fire. Indeed, various other lower-stem bark beetles, such as *Hylurgops* spp, *Hylastes* spp., and *Scierus* spp., were more abundant in burned stands, but they generally increased over time in both types of stands. In addition, upper-stem bark beetles increased in non-burned stands 3 years after fire at Upper Saskatchewan, in part due to *Pityogenes* spp., which are known to attack fire-injured trees (Rasmussen et al. 1996; Ryan and Amman 1996; Toivanen and Kotiaho 2007).

Our overall abundance analysis, which included all bark and ambrosia species, showed no differences between fire injury classes. Rather, I found an increasing abundance over time, complementing our individual group and species results. Thus, I conclude that fire can induce increasing abundances in some bark beetle species, and allow beetles to spread to non-burned areas. This may result in bark beetle outbreaks and mortality of healthy trees.

#### 4.4.2 What is the pattern of bark and ambrosia beetle progression into burned areas after fire?

All feeding groups were present in burned pine stands 1 year after fire, albeit at varying abundances relative to future years, indicating that there is no clear colonisation progression of groups after fire, but rather changing patterns of abundance. Upper-stem bark beetles were generally the most abundant insects 1 year after fire. This group includes the twig beetle genera *Pityogenes* and *Pityophthorus*, which have also been found to colonise burned *P. contorta* in Yellowstone National Park 1 year after fire (Amman and Ryan 1991). *Scolytus piceae*, a spruce engraver, is commonly found in stressed or weakened hosts including *P. contorta*, but there have been no other reports of increased abundances after fire (Bright 1976). *Ips latidens* colonises the tops of dead or dying trees including *P. contorta* (Bright 1976), and has been found in burned *Pinus ponderosa* (ponderosa pine) and *Pinus jeffreyi* (Jeffrey pine), albeit 2 years after fire (Fettig et al. 2008). In the absence of fire, upper-stem bark beetles generally infest stressed trees that have previously been attacked by lower-stem bark beetles or have experienced root herbivory (Aukema et al. 2010). It is possible that ground fire mimics this stress, attracting upper-stem bark beetles to the most injured trees immediately after fire.

Main-stem bark beetles and ambrosia beetles were generally the most abundant species 2 years after fire. Since bark and ambrosia beetles can be attracted to the pheromones of other species (Haber Kern and Raffa 2003), these beetles may have been responding to cues emitted by early colonisers in addition to any attraction provided by fire-injured trees. I found that *I. pini* was the most abundant main-stem bark beetle species, in line with Ryan and Amman (1996), who found that this species was the most common bark beetle infesting *P. contorta* 1–4 years after fire in Yellowstone National Park. Although ambrosia beetles were not main drivers of community differences, they

were found almost exclusively in burned stands; the representative *Trypodendron* spp. followed the general trend of increasing 2 years after fire. My results agree with studies showing that ambrosia beetles colonise dead or weakened trees (e.g., Kimmey and Furniss 1943; Lowell et al. 1992; Ryan and Amman 1996; Parker et al. 2006), but run counter to those that found ambrosia beetles to be among the earliest colonisers of fire-injured trees (e.g., Hadfield and Magelssen 2006). Ambrosia beetles have recently and uncharacteristically been found to colonise healthy trees (Kühnholz et al. 2003) and are associated with some major tree diseases, such as sudden oak death in California (McPherson et al. 2008, 2013). If this trend continues, their tendency to be increase in burned stands and potentially build up populations may cause increased post-fire tree mortality.

In addition to main-stem bark beetles, lower-stem bark beetles were generally the most abundant species in burned stands 3 years after fire. Main-stem bark beetles seem to have maintained or increased their abundance, providing evidence for potential outbreaks. Lower-stem bark beetles, however, only showed an increase 3 years after fire relative to other groups. The most injured trees had already died during the first 2 years after fire (Chapter 2 of this thesis), so lower-stem bark beetles likely relied mainly on pheromones emitted by beetles that had colonised fire-injured trees in the first 2 years. *Hylastes longicollis* and *D. murrayanae* were the most abundant lower-stem bark beetle species, especially 3 years after fire. *Hylastes longicollis* feeds on aged, rather than fresh, phloem (Wood 1982; Lindgren and Miller 2002), and Miller et al. (1986) demonstrated attraction to stressed *P. contorta* for this species. Although *Hylastes* are not generally considered tree-killing beetles, they can occasionally cause host death (Furniss and Carolin 1977), and this may be intensified if trees are already injured by fire.

### 4.4.3 Can bark and ambrosia beetles affect *Dendroctonus ponderosae* colonisation of burned areas?

Bark and ambrosia beetles increased after fire, likely leading to increased competition with *D. ponderosae*, and resulting in population decline after an initial pulse. This hypothesis is consistent with studies that found *D. ponderosae* to be a poor competitor (Rankin and Borden 1991; Safranyik and Carroll 2006). Indeed, I found differences in the bark and ambrosia beetle community between areas with and without *D. ponderosae* at Mt. Nestor and the Ya Ha Tinda Ranch, and an interaction between *D. ponderosae* presence and year after fire at Upper Saskatchewan. At the first two sites, I caught approximately twice the number of bark and ambrosia beetles in areas with *D. ponderosae*, in agreement with Amman and Ryan (1991), who found that all trees attacked by *D. ponderosae* after fire also hosted other bark beetle species. This likely indicates that both *D. ponderosae* and the bark beetles observed here are attracted to similar stressed hosts, which increases the likelihood of competition. Another potential consequence for *D. ponderosae* in areas with increased numbers of competitors is increased predator and parasitoid loads, i.e., apparent competition; (Morris et al. 2005), as some natural enemies such as clerid predators are attracted to a wide variety of prey semiochemicals (Costa and Reeve 2011). Overall, increased competition seems a likely mechanism to explain why an initial increase in *D. ponderosae* attacks did not result in a long-term population increase after prescribed fire.

### 4.4.4 Conclusions

Taken together, our results show that members of the bark and ambrosia beetle community are generally attracted to burned *P. contorta* stands, likely responding to a combination of host cues indicating stress from fire injury and pheromones emitted



by conspecifics or closely-related species. This attraction seems to lead to increases in abundance over time for some species in both burned and adjacent non-burned stands, which might lead to population outbreaks under appropriate circumstances (e.g., enough injured hosts, enough beetles to take advantage of the resource pulse, species capable of outbreak, other disturbances, etc.). Furthermore, these patterns are opposite to those we observed for *D. ponderosae* in a previous study (Tabacaru et al. unpublished data; Chapter 2 of this thesis), where *D. ponderosae* colonisation either decreased over time or remained very low, indicating that increasing competitor populations likely negatively affect this tree-killing species after fire when it is at low-density populations. Overall, increased competition seems a likely mechanism to explain why an initial increase in *D. ponderosae* attacks did not result in a long-term population increase after prescribed fire.

# Chapter 5

## Passive traps set directly on host trees catch more subcortical insects than passive flight intercept traps

### 5.1 Introduction

Subcortical insects, those that use the inner bark of trees as habitat, include some of the most economically and ecologically important forest species in the world (Eidmann 1992; Erbilgin and Raffa 2002; Kurz et al. 2008; Raffa et al. 2008; Wermelinger et al. 2008; Saab et al. 2014). Bark beetles make up a large portion of these species; for example, the recent *Dendroctonus ponderosae* Hopkins (mountain pine beetle) outbreak in western North America has resulted in 50% mortality of merchantable pine in British Columbia, Canada over the last decade (Natural Resources Canada ). Thus, along with their natural enemies and competitors, bark beetles are frequently the focus of studies examining forest health and disturbance (e.g., Kurz et al. 2008; Safranyik et al. 2010; Powell et al. 2012).

Such studies often use traps to determine population dynamics, competition, host selection, or simply an inventory of species present in an area. Trapping subcortical insects using semiochemicals (i.e., chemicals that mediate interactions between organisms), such as insect pheromones and/or host tree chemicals, is the most common method used by researchers because it allows for a large number of individuals to be caught (e.g., Weslien et al. 1989; Erbilgin and Raffa 2001). As such, many studies have compared the efficiencies of baited traps, especially with respect to combinations of different semiochemicals such as pheromones and host chemicals, in trapping specific or closely related species (e.g., Erbilgin and Raffa 2000; Erbilgin et al. 2001; Brockerhoff et al. 2006; Xie and Lv 2013). However, baited traps may artificially aggregate insects, inflating abundance and possibly misrepresenting species richness in a given location. Furthermore, insects show geographical variation in their attraction to the same semiochemicals (e.g., Miller et al. 1997; Erbilgin et al. 2007), and the attraction range of these chemicals may be low or subject to perturbation, for example by wind, so that even traps baited with the same chemicals may catch different abundances of insects (e.g., Byers et al. 1989; Sufyan et al. 2011). As such, when the goal is to determine species richness and abundances, or to compare among sites, baited traps may confound results. Thus, if one is interested in the extent of a species' range or in determining community differences between disturbance types, passive traps that collect insects already in the area are necessary.

Although trap characteristics other than bait type, such as colour and placement, are influential in all cases (Dubbel et al. 1985; Ulyshen and Hanula 2007; Crook et al. 2014), they become extremely important when baits are not involved. However, although it is important to understand the effects of passive trap type on catch efficiency, comparisons are rare in the literature (but see Safranyik et al. 2004b; Ulyshen and Hanula 2007; DeZan et al. 2014). In a previous related study, I examined the rela-

tionship between *D. ponderosae* and its natural enemies and competitors in post-fire pine forests. Since I intended to compare the subcortical community between burned and non-burned areas, I used several types of passive traps to collect as many species as possible. Here, I report differences among our passive traps with respect to abundances of a wide variety of subcortical families and species, with the objective to test whether trap type affects catch efficiency. I also compared the efficiencies of two types of traps which both target flying insects at similar heights, but differ in their placements: landing traps are placed directly on host trees and flight intercept traps are hung between trees. Furthermore, because I found that post-fire pine forests hosted more subcortical insects (Tabacaru and Erbilgin 2015; Chapter 3 of this thesis), and some insects can change their behaviour at higher densities (e.g., *D. ponderosae*; Safranyik et al. 2010), I examined fire injury and trap type interactions. Our results will aid researchers in their choice of trap type and add to a much-needed reference collection of passive trap comparisons.

## **5.2 Materials and methods**

### **5.2.1 Study sites and fire injury classes**

I set traps in three mature *P. contorta* forests within the Alberta Rocky Mountains, which were burned in spring 2009: Mt. Nestor (115° 22'55.617" W, 50° 54'25.073" N; elevation of centre 1800 m), Upper Saskatchewan (116° 37'2.310" W, 52° 1'17.964" N; elevation of centre 1400 m), and the Ya Ha Tinda Ranch (115° 36'35.079" W, 51° 44'07.784" N; elevation of centre 1700 m). These forests were separated by > 100 km. Because our original study focussed on the effect of prescribed fire on *D. ponderosae* and its associated community, I categorised fire injury into three classes: non-burned, low, and moderate, defined using Parks Canada burn severity classifications (Soverel

et al. 2010). I then used ArcGIS 9.2 (ESRI, Redlands, CA, U.S.A.) to randomly locate at least 15 10×10-m plots, placed a minimum of 200 m apart in each fire injury class at each site.

### **5.2.2 Trap types and insect collection**

I used three types of passive traps (i.e., without attractants): emergence (Fig. 3.1), landing (Fig. 3.2), and flight intercept (Fig. 3.3). I set up 3–5 traps of each type in each fire injury class at each site for 3 consecutive years (2010–2012). They were put up in late May and collected once at the end of the season in late August. Because several traps were destroyed by animals during sampling, I used the catches of 71 emergence traps, 81 landing traps, and 102 flight intercept traps.

For emergence traps, I cut mesh cloths (< 0.5 mm) into 1 × 2 m-squares with 2-m triangles sowed into funnels. These were wrapped around tree trunks between heights of 1 and 2 m. I then attached 105-mL urine sample cups (lids were drilled to leave only the frame), filled with 10 mL of 50% propylene glycol solution diluted with water, to the bottoms of the cloth funnels using standard pipe clamps. Lids were used because cups were too flimsy to hold the pipe clamps. During collection, cups were removed and sealed with new, non-drilled lids. Every new season, emergence traps were moved to new trees within the same plot to avoid excluding insects.

For landing traps, I cut the bottoms of clear 2 L-soda bottles, and cut the bottles in half, length-wise. I then glued drilled threaded lids to the inverted bottle tops, which became funnels. Finally, I attached 105 mL-plastic sample cups filled with 10 mL of 50% propylene glycol solution, diluted with water to the bottle tops. Landing traps were attached to tree trunks at breast height (1.3 m from the forest floor). For collection, cups were removed as for emergence traps. I did not use sticky traps because I intended to identify physically fragile individuals, such as Hymenoptera. Landing

traps were always placed on live trees, and were moved year to year only if trees had died over the winter.

Lastly, I hung flight intercept panel traps (Advanced Pheromone Technologies, Marylhurst, OR, U.S.A.) between two trees, at least 1 m off the ground using rope. I filled collection cups with 50 mL of 50% propylene glycol solution, diluted with water. For collection, cups were removed and all liquid was poured into 1 L Nalgene bottles (Thermo Fisher Scientific Inc., Waltham, MA, U.S.A.). I determined the area of each trap type, in order to standardise insect abundances among traps. Emergence traps were  $\sim 1$  m<sup>2</sup>, landing traps were  $\sim 0.057$  m<sup>2</sup>, and flight intercept traps were  $\sim 0.94$  m<sup>2</sup>. Flight intercept traps were left in the same locations year to year.

Following field collection, I sorted, identified, and stored insects in a 70% ethanol solution. I identified 5,243 individuals pertaining to the subcortical community to 31 families, as well as one sub-family in three orders, Coleoptera, Diptera, and Hymenoptera, based on the potential interactions with *D. ponderosae* reported in the literature (e.g., Kenis et al. 2004). I then grouped insect families into three functional groups (herbivores, predators, and parasitoids) to identify any potential relationships among trap type and life-history characteristics. For the sub-family Scolytinae (Coleoptera: Curculionidae), I identified individuals to species or genera. For the purposes of discussing family-level analyses, I will be referring to Scolytinae as a family.

### 5.3 Statistical analyses

All statistical analyses were performed using R version 3.0.2 (R Development Core Team 2013). Any family occurring in  $< 5\%$  of traps in any given family-level analysis was removed from that analysis. All abundances were then standardised to account for differences in the number of trapping days and areas of each trap type. I did not use

emergence traps in statistical analyses because they are restricted to the community that specifically emerges from under the bark during the time of year that our traps were used. Rather, I statistically compared trap catches of landing and flight intercept traps because they can potentially catch the same flying insects.

I first used six linear mixed-effect models (*lme4* and *lmerTest* packages in R) with site and year as random effects to determine if there was an interaction between effects of trap type and fire injury class (burned vs. non-burned) on standardised abundances (number/trap/day/m<sup>2</sup>) of Coleoptera, Diptera, Hymenoptera, herbivores, predators, and parasitoids. If I found no interaction, I performed additional linear mixed-effect models, this time with fire injury class nested within site and year as random effects to determine the effect of trap type on standardised insect abundances. Then, to graphically visualise how trap types are associated with specific insect families within each order, I used Nonmetric Multidimensional Scaling (NMDS; *ecodist* package in R), an ordination method well-suited to community data with many zeroes (McCune and Grace 2002). I used the Bray-Curtis dissimilarity as a distance measure, with which distances between samples were ranked. These were then represented in a low-dimensional configuration which minimises stress, a measure of how well the configuration displays more similar points closer together. In addition, I used a linear mixed-effect model to determine the effect of trap type on standardised abundances of Scolytinae, comprised of the bark and ambrosia beetles. Again, I used NMDS with the Bray-Curtis dissimilarity to visualise how trap types are associated with specific species in this group.

In this chapter, I considered significance at both  $\alpha = 0.05$  and  $\alpha = 0.1$  because, although the probability of Type I error increases with increasing values of  $\alpha$ , prescribed fire is a complicated management technique affecting many aspects of forest ecosystems, and the consequences of not considering bark beetle responses when they occur are arguably greater than those of erroneously concluding that they exist.

## 5.4 Results

Emergence, landing, and flight intercept traps caught 66%, 81%, and 84% of the total number of families (Tables 5.1 and 5.2). Additionally, they caught, 45%, 68%, and 87% of the total number of scolytin species/genera (Tables 5.3 and 5.4).

I found no interactions between trap type and fire injury class for any order or functional group. When fire injury class was considered a random effect, all three orders (Coleoptera, Diptera, and Hymenoptera) showed differences between landing and flight intercept traps, wherein landing traps caught more individuals per unit area than flight intercept traps (Coleoptera:  $F_{1,181} = 3.01$ ,  $P = 0.066$ ; Diptera:  $F_{1,176.7} = 3.60$ ,  $P = 0.058$ ; Hymenoptera:  $F_{1,177.3} = 4.06$ ,  $P < 0.05$ , significant at  $\alpha = 0.1$ ). However, when families were divided into functional groups, I found no differences between landing and flight intercept traps for herbivores and predators (both  $P > 0.1$ ). Parasitoids, a group comprised of almost the same families as the group Hymenoptera, differed between trap types ( $F_{1,177.9} = 3.56$ ,  $P = 0.061$ ), wherein landing traps again caught more individuals per unit area than flight intercept traps.

In general, 66% of families were shared between landing and flight intercept traps. For Coleoptera, NMDS (two axes, stress < 0.3) showed that all families were associated with landing traps, compared to flight intercept traps (Fig. 5.1). For Diptera, NMDS (two axes, stress < 0.3) showed that all families were again associated with landing traps, although Empididae showed only marginal associations (Fig.5.2). For Hymenoptera, NMDS (two axes, stress < 0.3) showed that Siricidae, Braconidae, and Scelionidae were strongly associated with landing traps, Ceraphronidae and Ichneumonidae were weakly associated with landing traps, and Platygasteridae and Pteromalidae were associated with flight intercept traps. Diapriidae appeared to not be associated with a particular trap type (Fig. 5.3). Families that were found exclusively in one trap type all belonged to the order Hymenoptera and were as follows: Chalcidae (flight intercept),



Table 5.1: Standardised mean abundances (nr/trap day) of insects, divided among three trap types. Insects were collected at three sites, over 3 years. Traps were set in *Pinus contorta* forests in Alberta, Canada. Empty cells represent zero values. Zeroes represent non-zero values that have been rounded to zero.

	<b>Emergence</b>	<b>Landing</b>	<b>Flight intercept</b>
	nr/trap day	nr/trap day	nr/trap day
<b>Order Coleoptera</b>			
Buprestidae		0.000	0.000
Cerambycidae	0.006	0.011	0.035
Cleridae	0.002	0.016	0.019
Scolytinae (sub-family)	0.186	0.096	0.176
Staphylinidae	0.074	0.066	0.055
Trogossitidae	0.003	0.000	0.002
<b>Order Diptera</b>			
Asilidae		0.001	0.000
Dolichopodidae	0.008	0.018	0.004
Empididae	0.006	0.003	0.011
Lonchaeidae	0.003	0.014	0.089
Xylophagidae		0.001	0.000
<b>Order Hymenoptera</b>			
Braconidae	0.004	0.002	0.006
Ceraphronidae	0.001	0.000	0.002
Chalcididae			0.000
Cynipidae			0.000
Diapriidae	0.002	0.000	0.002
Encyrtidae	0.001	0.000	0.001
Eucharitidae			0.000
Eucoilidae		0.000	
Eulophidae	0.000		0.000
Eupelmidae		0.000	
Eurytomidae	0.001	0.000	0.001
Ichneumonidae	0.002	0.005	0.015
Liopteridae		0.000	
Megaspilidae		0.000	
Mymaridae	0.000	0.000	0.000
Platygastridae	0.000		0.003
Proctotrupidae	0.000		0.001
Pteromalidae	0.001	0.001	0.005
Scelionidae	0.003	0.001	0.003
Siricidae		0.002	0.001
Torymidae	0.001	0.000	

Table 5.2: Standardised mean abundances (nr/trap day/m<sup>2</sup>; i.e., per surface area) of insects, divided among three trap types. Insects were collected at three sites, over 3 years. Traps were set in *Pinus contorta* forests in Alberta, Canada. Empty cells represent zero values. Zeroes represent non-zero values that have been rounded to zero.

	<b>Emergence</b>	<b>Landing</b>	<b>Flight intercept</b>
	<u>nr/trap day/m<sup>2</sup></u>	<u>nr/trap day/m<sup>2</sup></u>	<u>nr/trap day/m<sup>2</sup></u>
<b>Order Coleoptera</b>			
Buprestidae		0.003	0.000
Cerambycidae	0.006	0.192	0.037
Cleridae	0.002	0.276	0.020
Scolytinae (sub-family)	0.186	1.689	0.187
Staphylinidae	0.074	1.165	0.059
Trogossitidae	0.003	0.003	0.002
<b>Order Diptera</b>			
Asilidae		0.012	0.000
Dolichopodidae	0.008	0.320	0.005
Empididae	0.006	0.044	0.012
Lonchaeidae	0.003	0.250	0.095
Xylophagidae		0.011	0.000
<b>Order Hymenoptera</b>			
Braconidae	0.004	0.038	0.006
Ceraphronidae	0.001	0.003	0.002
Chalcididae			0.000
Cynipidae			0.000
Diapriidae	0.002	0.007	0.002
Encyrtidae	0.001	0.007	0.001
Eucharitidae			0.000
Eucoilidae		0.003	
Eulophidae	0.000		0.000
Eupelmidae		0.003	
Eurytomidae	0.001	0.003	0.001
Ichneumonidae	0.002	0.093	0.016
Liopteridae		0.003	
Megaspilidae		0.007	
Mymaridae	0.000	0.003	0.000
Platygastridae	0.000		0.003
Proctotrupidae	0.000		0.001
Pteromalidae	0.001	0.024	0.005
Scelionidae	0.003	0.009	0.003
Siricidae		0.036	0.001
Torymidae	0.001	0.004	

Table 5.3: Standardised mean abundances (nr/trap day) of bark beetles (Curculionidae: Scolytinae), divided among three trap types. Insects were collected at three sites, over 3 years. Traps were set in *Pinus contorta* forests in Alberta, Canada. Empty cells represent zero values. Zeroes represent non-zero values that have been rounded to zero.

	<b>Emergence</b>	<b>Landing</b>	<b>Flight intercept</b>
	nr/trap day	nr/trap day	nr/trap day
<i>Dendroctonus murrayanae</i>	0.002	0.007	0.005
<i>Dendroctonus ponderosae</i>	0.000		0.000
<i>Dendroctonus rufipennis</i>	0.000	0.001	0.001
<i>Dendroctonus valens</i>		0.000	0.000
<i>Dendroctonus</i> spp.	0.000	0.001	0.001
<i>Dryocoetes affaber</i>		0.000	
<i>Dryocoetes autographus</i>	0.000	0.001	0.003
<i>Dryocoetes</i> spp.			0.000
<i>Gnathotrichus</i> spp.			0.000
<i>Hylastes gracilis</i>		0.002	0.001
<i>Hylastes longicollis</i>	0.004	0.013	0.007
<i>Hylastes nigrinus</i>		0.000	
<i>Hylastes porosus</i>			0.001
<i>Hylastes ruber</i>		0.000	0.001
<i>Hylastes</i> spp.			0.000
<i>Hylurgops porosus</i>	0.001	0.006	0.008
<i>Hylurgops rugipennis</i>	0.000	0.006	0.004
<i>Hylurgops</i> spp.	0.000		0.000
<i>Ips emarginatus</i>		0.000	
<i>Ips latidens</i>	0.008	0.017	0.006
<i>Ips perturbatus</i>		0.000	0.000
<i>Ips pini</i>	0.063	0.008	0.034
<i>Ips</i> spp.	0.000	0.001	0.001
<i>Orthotomicus caelatus</i>			0.000
<i>Pityogenes</i> spp.	0.000	0.006	0.038
<i>Pityokteines minutus</i>			0.002
<i>Pityophthorus</i> spp.	0.002	0.002	0.004
<i>Polygraphus rufipennis</i>	0.000	0.000	0.002
<i>Pseudips mexicanus</i>		0.000	
<i>Pseudopityophthorus</i> spp.			0.000
<i>Scierus annectens</i>	0.000		0.001
<i>Scierus pubescens</i>			0.000
<i>Scolytus piceae</i>			0.002
<i>Scolytus</i> spp.			0.000
<i>Trypodendron</i> spp.	0.011	0.002	0.018
<i>Xyleborus xylographus</i>			0.000
<i>Xylechinus montanus</i>		0.000	0.001

Table 5.4: Standardised mean abundances (nr/trap day/m<sup>2</sup>; i.e., per surface area) of bark beetles (Curculionidae: Scolytinae), divided among three trap types. Insects were collected at three sites, over 3 years. Traps were set in *Pinus contorta* forests in Alberta, Canada. Empty cells represent zero values. Zeroes represent non-zero values that have been rounded to zero.

	Emergence	Landing	Flight intercept
	nr/trap day/m <sup>2</sup>	nr/trap day/m <sup>2</sup>	nr/trap day/m <sup>2</sup>
<i>Dendroctonus murrayanae</i>	0.002	0.131	0.006
<i>Dendroctonus ponderosae</i>	0.000		0.000
<i>Dendroctonus rufipennis</i>	0.000	0.017	0.002
<i>Dendroctonus valens</i>		0.005	0.000
<i>Dendroctonus</i> spp.	0.000	0.011	0.000
<i>Dryocoetes affaber</i>		0.002	
<i>Dryocoetes autographus</i>	0.000	0.011	0.003
<i>Dryocoetes</i> spp.			0.000
<i>Gnathotrichus</i> spp.			0.000
<i>Hylastes gracilis</i>		0.037	0.001
<i>Hylastes longicollis</i>	0.004	0.233	0.007
<i>Hylastes nigrinus</i>		0.002	
<i>Hylastes porosus</i>			0.001
<i>Hylastes ruber</i>		0.006	0.001
<i>Hylastes</i> spp.			0.000
<i>Hylurgops porosus</i>	0.001	0.096	0.008
<i>Hylurgops rugipennis</i>	0.000	0.105	0.004
<i>Hylurgops</i> spp.	0.000		0.000
<i>Ips emarginatus</i>		0.003	
<i>Ips latidens</i>	0.008	0.293	0.007
<i>Ips perturbatus</i>		0.003	0.000
<i>Ips pini</i>	0.063	0.138	0.036
<i>Ips</i> spp.	0.000	0.017	0.000
<i>Orthotomicus caelatus</i>			0.000
<i>Pityogenes</i> spp.	0.000	0.106	0.040
<i>Pityokteines minutus</i>			0.003
<i>Pityophthorus</i> spp.	0.002	0.039	0.004
<i>Polygraphus rufipennis</i>	0.000	0.006	0.002
<i>Pseudips mexicanus</i>		0.003	
<i>Pseudopityophthorus</i> spp.			0.000
<i>Scierus annectens</i>	0.000		0.001
<i>Scierus pubescens</i>			0.000
<i>Scolytus piceae</i>			0.003
<i>Scolytus</i> spp.			0.000
<i>Trypodendron</i> spp.	0.011	0.032	0.020
<i>Xyleborus xylographus</i>			0.000
<i>Xylechinus montanus</i>		0.003	0.002

Cynipidae (flight intercept), Eucharitidae (flight intercept), Eucoilidae (landing), Eupelmidae (landing), Liopteridae (landing), and Megaspilidae (landing). No family was found exclusively in emergence traps.

I did not find an interaction between trap type and fire injury class for Scolytinae. When fire injury class was used as a random effect, Scolytinae showed differences between landing and flight intercept traps ( $F_{2,248} = 2.65$ ,  $P = 0.072$ ), wherein landing traps caught more individuals per unit area than flight intercept traps; 57% of species/genera were shared between landing and flight intercept traps. NMDS (three axes, stress < 0.3) showed that all species but *Dryocoetes autographus* were associated with landing traps, although *Trypodendron* spp. showed only weak associations (Fig. 5.4; only axes 1 and 2 are displayed). Species/genera that were found exclusively in one type of trap are as follows: *Gnathotrichus* spp. (flight intercept), *Hylastes porosus* (flight intercept), *Orthotomicus caelatus* (flight intercept), *Pityokteines minutus* (flight intercept), *Pseudopityophthorus* spp. (flight intercept), *Scierus pubescens* (flight intercept), *Scolytus piceae* (flight intercept), *Xyleborus xylographus* (flight intercept), *Hylastes nigrinus* (landing), *Ips emarginatus* (landing). No species/genus was found exclusively in emergence traps.

## 5.5 Discussion

I found marked differences in catches among our trap types, both for subcortical Coleoptera, Diptera, and Hymenoptera families, and for Scolytinae species/genera. Although they both targeted flying insects, landing and flight intercept traps caught substantially different species, sharing only 66% and 57% of families and Scolytinae species/genera, respectively. Overall, our study reveals three important results: 1) landing traps catch more subcortical insects while flight intercept traps catch a wider variety

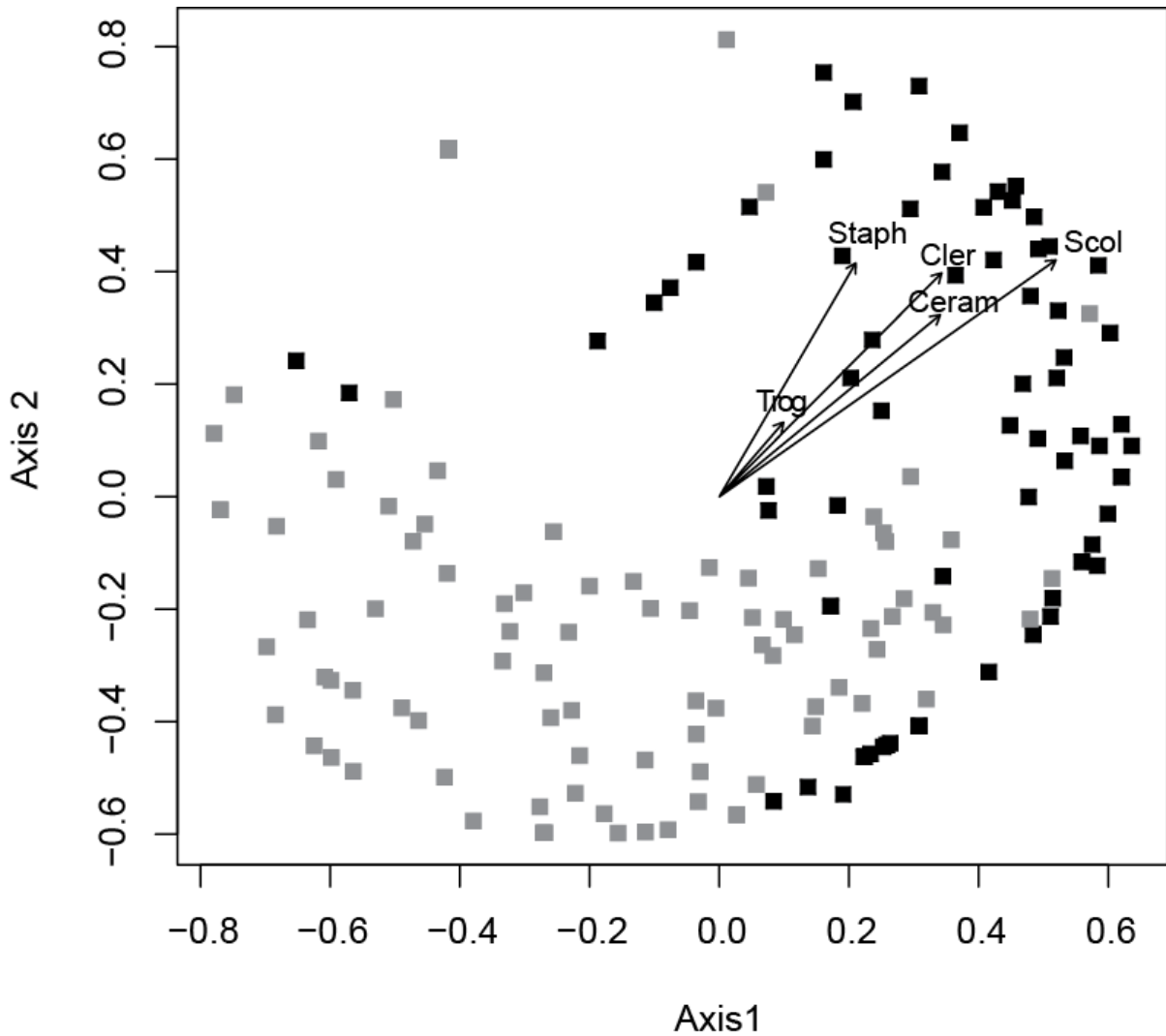


Figure 5.1: Visualisation of the effect of trap type on coleopteran families, using Non-metric Multidimensional Scaling (N-MDS). Traps were set in *Pinus contorta* forests in Alberta, Canada. Grey squares represent flight intercept traps and black squares represent landing traps (see text for descriptions). Ceram = Cerambycidae, Cler = Cleridae, Scol = Scolytinae, Staph = Staphilinidae, Trog = Trogossitidae.

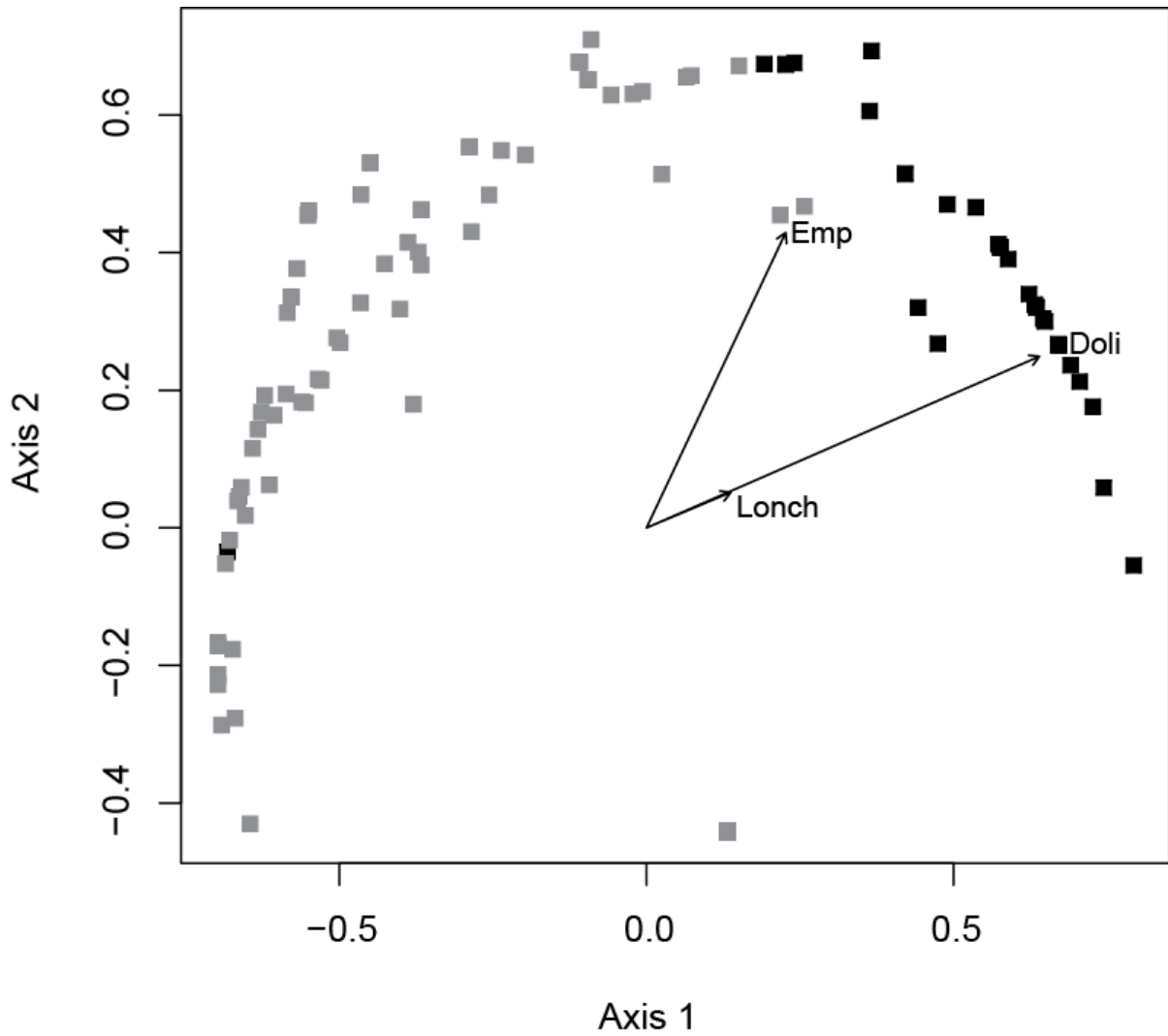


Figure 5.2: Visualisation of the effect of trap type on dipteran families, using Non-metric Multidimensional Scaling (NMDS). Traps were set in *Pinus contorta* forests in Alberta, Canada. Grey squares represent flight intercept traps and black squares represent landing traps (see text for descriptions). Emp = Empididae, Doli = Dolichopodidae, Lonch = Lonchaeidae.

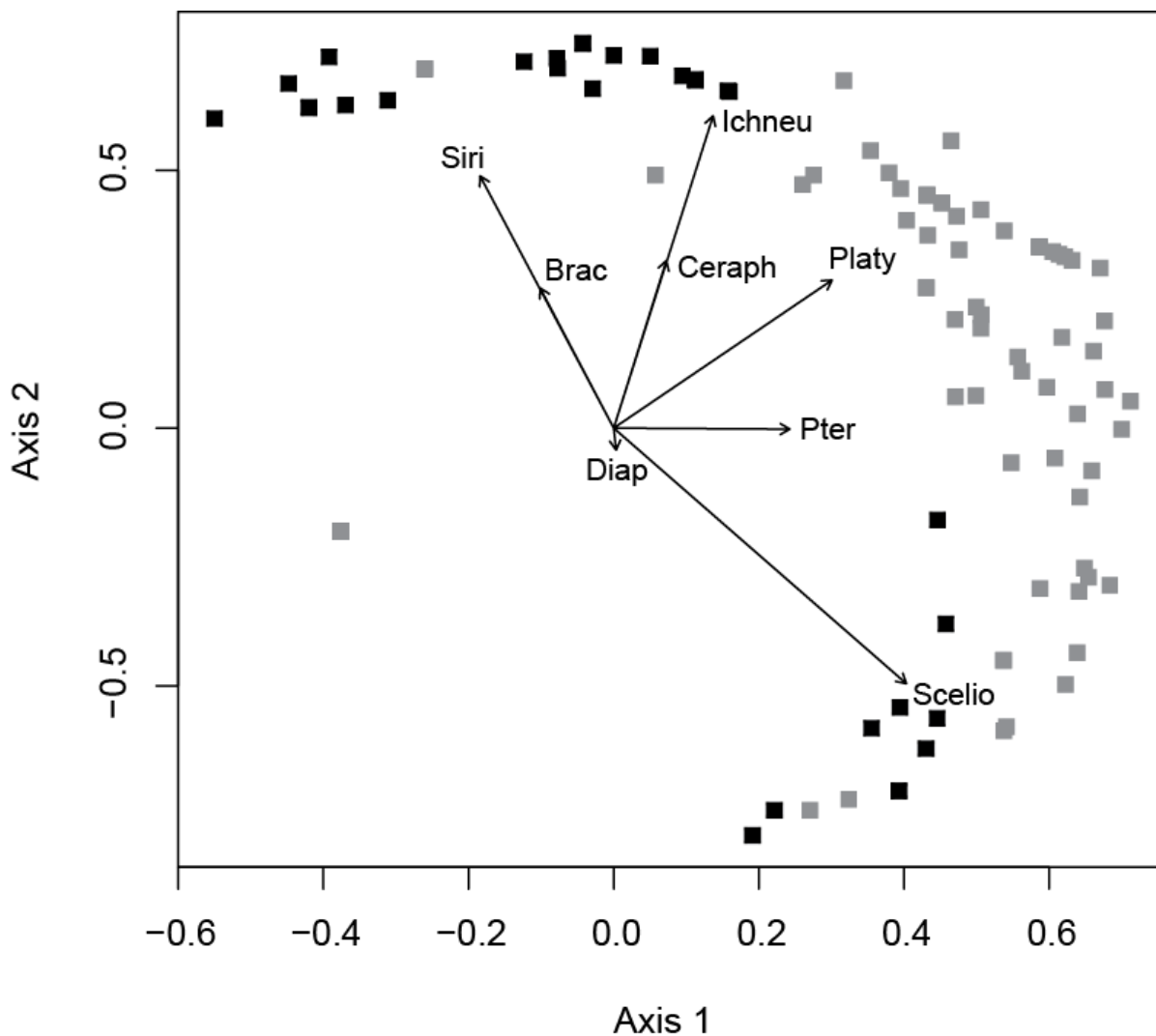


Figure 5.3: Visualisation of the effect of trap type on hymenopteran families, using Non-metric Multidimensional Scaling (NMS). Traps were set in *Pinus contorta* forests in Alberta, Canada. Grey squares represent flight intercept traps and black squares represent landing traps (see text for descriptions). Brac = Braconidae, Ceraph = Ceraphronidae, Diap = Diapriidae, Ichneu = Ichneumonidae, Platy = Platygasteridae, Pter = Pteromalidae, Scelio = Scelionidae, Siri = Siricidae.



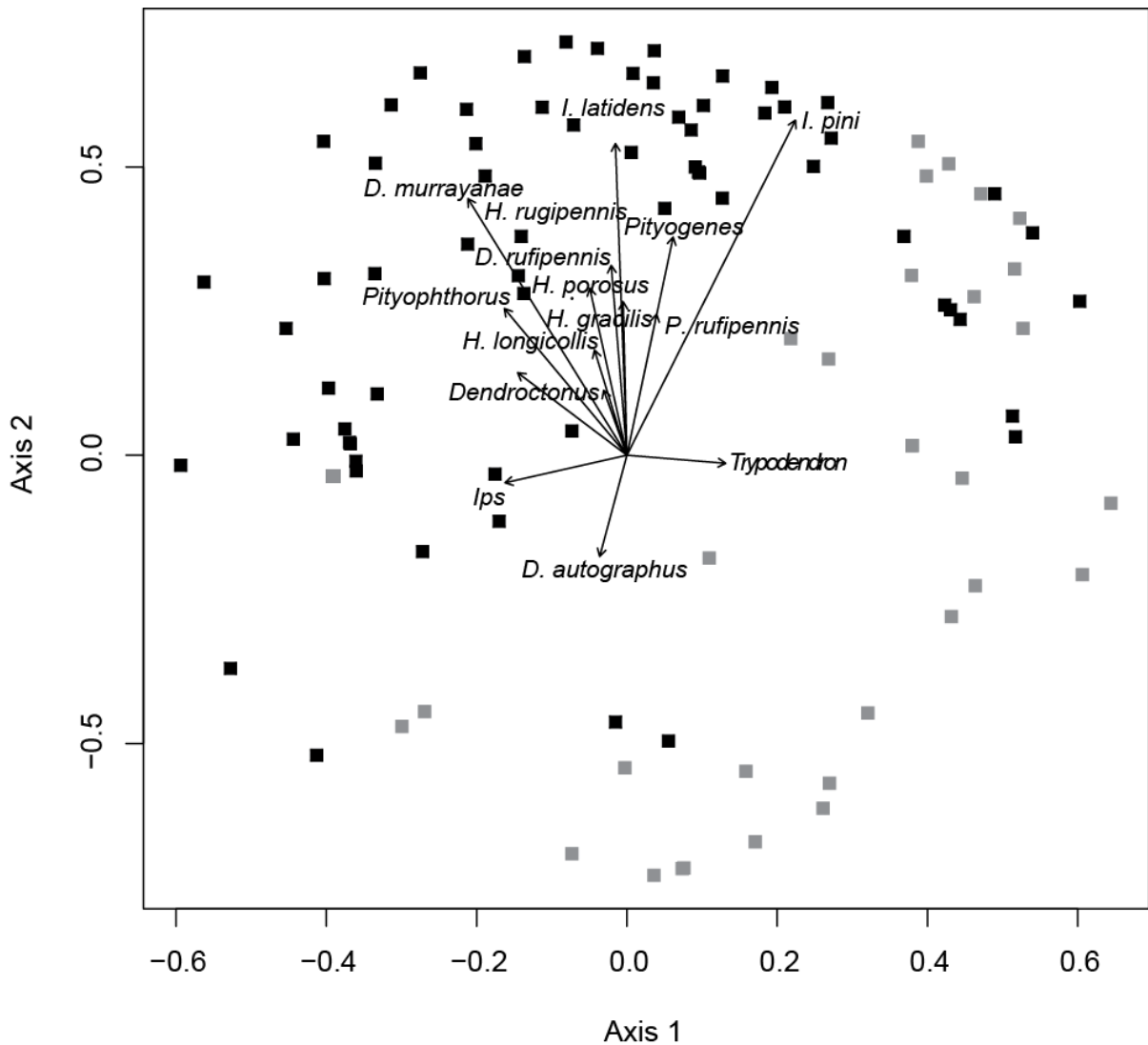


Figure 5.4: Visualisation of the effect of trap type on scolytin species, using Non-metric Multidimensional Scaling (NMDS). Traps were set in *Pinus contorta* forests in Alberta, Canada. Grey squares represent flight intercept traps and black squares represent landing traps (see text for descriptions). *D. autographus* = *Dryocoetes autographus*, *D. murrayanae* = *Dendroctonus murrayanae*, *D. rufipennis* = *Dendroctonus rufipennis*, *Dendroctonus* = *Dendroctonus* spp., *H. gracilis* = *Hylastes gracilis*, *H. longicollis* = *Hylastes longicollis*, *H. porosus* = *Hylurgops porosus*, *H. rugipennis* = *Hylurgops rugipennis*, *I. latidens* = *Ips latidens*, *I. pini* = *Ips pini*, *Ips* = *Ips* spp., *Pityogenes* = *Pityogenes* spp., *Pityophthorus* = *Pityophthorus* spp., *P. rufipennis* = *Polygraphus rufipennis*, *Trypodendron* = *Trypodendron* spp.

of species, 2) grouping species as herbivores, predators, and parasitoids obscures trap type effects, and 3) fire, a major disturbance that affects the subcortical community (Tabacaru and Erbilgin 2015; Chapter 3 of this thesis), does not interact with trap type. Below I discussed the importance and implications of these results in forest management.

First, I found that landing traps, the smaller of the two flight traps, almost always caught more insects when I accounted for surface area. This may be explained by the close proximity of the landing traps to host trees, as they likely provided visual and olfactory cues to flying insects. Although attraction to tree volatiles has been reported extensively in bark and ambrosia beetles (e.g., Tunset et al. 1993; Shore and Lindgren 1996), this is one of few studies reporting evidence for such attraction in Hymenoptera and Diptera. In support, Sullivan et al. (2000) reported that the bark beetle parasitoid *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae) is not attracted to host beetles that have been removed from trees. Thus, while vertical trap profiles are more successful than horizontal ones (Billings et al. 1976; Vité and Bakke 1979), using transparent traps on trees may further increase trap success. Simply enlarging a landing trap should increase its catch.

Although landing traps caught more individuals, flight intercept traps caught a wider variety of subcortical insect families and scolytin species/genera. At the family level, this difference is accounted for exclusively by hymenopteran parasitoids, several of which were caught in flight intercept traps but not in landing traps. Although there are several known parasitoid wasps associated with bark beetles in the families I identified (e.g., *Platygaster* spp., Boone et al. 2009; *R. xylophagorum*; Sullivan et al. 2000), most are large families that parasitise hosts living in various environments. It is possible that some of the individuals I identified were not predominantly associated with subcortical habitat and thus were caught opportunistically in flight intercept traps. I

also caught several species/genera within the sub-family Scolytinae, e.g., *Scierus* spp., only in flight intercept traps. I suspect that placing traps on living *P. contorta* trees at breast height excludes various scolytins depending on their host preferences. For example, although *Scierus annectens* can colonise *P. contorta*, *Picea* spp. are its main hosts, and *Scierus pubescens* mainly infests *Abies* and *Picea* spp. (Furniss and Carolin 1977). Furthermore, given that bark beetles attack tree stems at varying heights (Paine et al. 1981), traps placed at breast height may have excluded some lower- or upper-stem colonising species. Lastly, some species such as ambrosia beetles (e.g., *Trypodendron* and *Xyleborus* spp.) prefer to colonise dead wood (Dyer and Chapman 1965), so they would not be predominantly attracted to live hosts.

Second, when I divided families into three functional groups (herbivores, predators, and parasitoids), only parasitoids differed between trap types because the members of this group closely resembled those of the group Hymenoptera. These results demonstrate that species characteristics such as flight paths and attack heights on host trees, rather than the species' ecological functions, differentiate trap efficiency for both herbivores and predators (e.g., Safranyik et al. 2000: flight paths differ among bark beetle species). This means that grouping by ecological roles (e.g., herbivore), is probably too broad to permit differentiation among trap types. That is, although herbivores all feed on plant tissue under the bark, their species-level preferences and characteristics are obscured when they are grouped.

Third, the effect of fire injury on the subcortical community did not interact with trap type effects. Although insects in the subcortical community were more abundant in burned stands relative to non-burned stands (Tabacaru and Erbilgin 2015; Chapter 3 of this thesis), species characteristics, such as host location behaviour, that differentiate trap catches were not affected by fire. These results explain why many so called secondary bark beetles, e.g., the majority of Scolytinae species, cannot reach outbreak

levels even after their populations increase (Lindgren and Raffa 2013). In contrast, aggressive species such as *D. ponderosae* and *Ips typographus* show density dependent host selection behaviours: they are associated with stressed trees at low densities, but colonise healthy trees at high densities (Safranyik et al. 2010).

Emergence traps also trapped a variety of insect families. I show that even large mesh funnels can entrap hymenopteran wasps, which are generally more delicate. However, emergence traps can potentially inhibit late brood parasitism and can thus affect the natural enemy complex emerging from host trees (McClelland et al. 1978). Our traps were set up in late May, when several bark beetle species are still in their pupal stages. This likely excluded some natural enemies, and may explain why emergence traps caught the fewest dipteran and hymenopteran families.

I conclude that when targeting insects associated with subcortical habitat, clear passive traps placed directly on host trees capture more individuals per unit of trap area than intercept traps hung between trees. Additionally, I submit that a combination of trap types should be used when the goal is to characterise the community of subcortical insects, because species that prefer either different parts of the host or different hosts altogether may still be present. In addition, I add to the body of literature showing that subcortical insects use more than physical forms to detect trees. Finally, it is vital to account for area when comparing trap types: flight intercept traps caught more insects, but this was simply due to their larger size. Overall, I show that passive trap types differ significantly in their catch, and it is therefore extremely important to develop a repository of passive trap comparisons with respect to a wide variety of insect species.

# Chapter 6

## Conclusions

In this thesis, I have described the events following prescribed fire in *P. contorta* forests with respect to the subcortical insect community and, in particular, one aggressive bark beetle, *Dendroctonus ponderosae* Hopkins (mountain pine beetle). Fire and insects are the primary disturbance types in western North American conifer forests (Romme and Knight 1982), and prescribed fire is increasingly used as a forest management technique (White et al. 2011; Ryan et al. 2013), especially in protected areas. Thus, it is important both ecologically and economically to understand the role of fire in the population dynamics of *D. ponderosae*, the most significant insect in western North American forests (Amman and Baker 1972; Li et al. 2005; Bentz et al. 2010).

I first examined whether fire-injured host trees were more attractive to *D. ponderosae* than non-burned trees. I showed that proportionally more fire-injured trees were attacked than non-burned trees every year for 4 years after fire. In addition, more beetles attacked each tree in burned than in non-burned stands. My results are consistent with the established understanding of *D. ponderosae*-host tree interactions at low-density populations, when beetles generally attack weakened, stressed trees (Safranyik et al. 2010).

Assuming that fire-injured trees are preferentially attacked, two hypotheses have been proposed to explain how fire ultimately affects low-density populations of primary bark beetles: 1) fires trigger population growth, shifting a population to outbreak levels (Rasmussen et al. 1996; McHugh et al. 2003), or 2) fires initially cause beetles to congregate, but subsequently create an environment in which initially high populations decline (Miller and Patterson 1927; Powell et al. 2012). Using attack data over 4 years, I showed that prescribed fire likely does not promote outbreaks of *D. ponderosae*. At one of three sites, although proportionally more fire-injured trees were attacked than non-burned trees, the proportion of trees attacked declined after the beetles first responded to an initial resource pulse. At the remaining two sites, although I did not observe a clear response to a pulsed resource, the proportion of trees attacked remained very low over time. The pattern was very similar at all sites when I examined the number of attacks per tree, indicating that beetle populations did not increase over time. Additionally, neither the proportion of trees attacked nor the number of attacks per tree increased in number in adjacent non-burned stands, which would have indicated population increase.

These responses add to our understanding of the population dynamics of primary bark beetles and of disturbance interactions in forest ecosystems. Because I observed what appears to be a stabilisation of *D. ponderosae* colonisation 4 years after fire at Mt. Nestor, and ongoing low rates of attack at the remaining sites, fires may serve as refugia for low-density populations of *D. ponderosae*. Without fire, these beetles would need other sources of weakened trees to avoid local extinction. These results support the proposal made by Powell et al. (2012), after they examined *D. ponderosae* attacks 1 year after wildfire. Thus, fire does not promote outbreaks but does help the beetles remain part of the ecosystem.

However, given our knowledge of *D. ponderosae* at low-density populations, i.e., that they are restricted to weakened hosts such as those injured by fire and thus should be able to take advantage of a large number of such trees, my results beg the question: why is it that fires do not promote outbreaks? Determining the mechanisms inhibiting *D. ponderosae* population increase following a new availability of hosts is critical to understanding the factors regulating their population dynamics in burned stands. First, I measured phloem nitrogen and moisture in fire-injured trees to assess resource quality due to their importance to bark beetle reproduction and survival (Redmer et al. 2001; Goodsman et al. 2012). Fire changes the availability of nitrogen to plants, perhaps decreasing the nutritional value of phloem in burned trees by altering nitrogen availability to plants (Powell et al. 2012), and burned trees may become too dry for bark beetle attack (DeNitto et al. 2000). However, I found that with respect to phloem nitrogen concentrations, burned trees always represented an equal or better quality resource than non-burned trees, both 1 and 3 years after fire. In addition, phloem moisture in fire-injured trees was similar to that of non-burned trees in both years. This indicates that reduced resource quality is likely not the main mechanism explaining beetle colonisation decline in post-fire *P. contorta* stands. Reduced resource quantity, however, represents a more likely contending mechanism, as the number of susceptible hosts rapidly declined in burned stands. Beetles seemed to prefer the most injured trees, but these initially died at a much faster rate than did less fire-injured trees. A rapid decline in resource quantity may thus have negatively affected *D. ponderosae* population growth, as emerging beetles were limited in finding suitable hosts.

Next, because *D. ponderosae* is associated with a diverse subcortical insect community of competitors, predators, and parasitoids that may influence their numbers at low-density populations (Safranyik and Carroll 2006; Boone et al. 2008), I examined whether *D. ponderosae* responses to fire-injured hosts are mediated by community in-

teractions. Using a whole-community approach, I showed that interactions between *D. ponderosae* and their insect competitors and predators are likely intensified in burned stands, as these groups were common in post-fire areas. Thus, although *D. ponderosae* can take advantage of fire-injured hosts immediately after fire, their competitors and predators colonise burned stands soon after and probably contribute to keeping their populations low. Finally, direct competitors, i.e., other bark beetles, seemed to be the group most associated with burned stands, and *D. ponderosae* is known to be a poor competitor (Rankin and Borden 1991; Safranyik and Carroll 2006). Thus, I examined the responses of the bark and ambrosia beetle community to fire and how this array of species might affect *D. ponderosae*. I divided these species according to their feeding preferences and found that all groups (lower-, upper-, and main-stem bark beetles and ambrosia beetles) occurred more often in burned than non-burned stands, and that some species increased in abundance over time. Ultimately, I provided evidence that *D. ponderosae* experiences increased competition soon after arriving in burned stands.

To conclude, there appear to be two important negative feedbacks that work to suppress any advantage the beetles may have in suddenly having access to susceptible hosts after fire. First, the seemingly preferred most-injured host trees are only widely available immediately after fire. Even if there are enough beetles to take advantage of this availability, as I observed at Mt. Nestor, the significant decrease in hosts over the first winter means that offspring likely incur high mortality searching for new trees the following summer. Second, the influx of secondary bark beetles and predators intensifies interspecific competition and predation, respectively. This combination is probably too strong a population suppressant for *D. ponderosae* to recover and increase in number. Thus, increased inter-species interactions combined with a rapid decrease in susceptible hosts likely contribute to *D. ponderosae*'s inability to rise to outbreak population levels after fire.



These results are likely broadly applicable to other primary bark beetles, but caution must be taken in predicting post-fire responses in other systems. For example, other species of pine such as *Pinus ponderosa*, have thicker bark and likely require more severe fires to become as susceptible to beetles as *P. contorta*. Additionally, slightly different tree compositions will host different communities of subcortical insects, including competitors, predators, and parasitoids of primary bark beetles.

Throughout this study, I used passive insect traps to obtain representations of the subcortical communities present in burned and adjacent non-burned stands. Passive traps were important in this case because using attractant lures would have artificially aggregated insects and mixed the communities from local and adjacent stands, possibly misrepresenting abundance and species data. Because there are few passive trap comparisons in the literature, I used three types of traps to gain as much information as possible about the communities in the area. I compared the efficiencies of these traps and found that landing traps, which are placed directly on host trees, catch more individuals per unit area than flight intercept traps. However, intercept traps catch a greater number of species, especially Hymenoptera. In addition, large emergence traps constructed of mesh cloth caught a variety of species, including fragile dipterans and hymenopterans.

## 6.1 Management implications

This study has provided evidence that *D. ponderosae* at low-density populations prefer fire-injured *P. contorta* trees in western Canada. Forest managers can expect to find an increased number of attacks on trees left alive shortly after a prescribed burn, either concentrated at the peripheries of large burned areas or in a mosaic throughout the burn, depending on fire severity and duration. However, I have shown that although

*D. ponderosae* does attack more burned trees, it is not able to build up its populations after fire. This means that managers can continue using prescribed fire for various goals in areas with low-density populations of *D. ponderosae* and not be concerned about promoting outbreaks. Caution must still be used, however, as interactions among disturbances were not examined here. For example, if fire occurred while or before trees became stressed from other disturbances such as drought or disease, results might differ. Managers may also wish to learn about the subcortical insects living in their forests, especially as members of this community cause the most post-fire tree mortality. In these cases I recommend the use of passive insect traps: landing traps for catching the greatest number of specific individuals, such as those that colonise their trees at mid-bole, or wherever the trap is placed, and a variety of trap types for surveying the subcortical community in general.

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