Effects of clear-cutting and wildfires on succession of ground beetle (Coleoptera: Carabidae) assemblages in western Alberta

by

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Abstract

I studied how carabid beetle assemblages in lodgepole pine stands have responded after clear-cut harvest and wildfires on an actively managed landscape ~20 km south of Hinton, Alberta. This work builds on and expands the focus of a previous study (Niemelä et al. 1993) conducted 23-24 years earlier in many of the same stands sampled in the current study. I compared carabid species assemblages along a chronosequence of stands ranging in age from 12 to 53 years after clear-cutting. Recovery of carabid assemblages toward preharvest structure in regenerating stands as reflected in the 2013-14 data appears to have been more rapid than in equivalently aged stands from the earlier study. In addition, species assemblages differed significantly between clear-cut and burned stands of comparable age in 2013-14. Specifically, carabid assemblages of younger burned stands show closer resemblance to assemblages in mature stands than harvested stands. This may indicate that recovery occurs faster in burned stands or that more old-growth species persist through burning compared to harvesting. Ground vegetation, mineral soil cover and basal area of trees and shrubs were significantly correlated with structure of carabid species assemblages in young and old regenerating stands after disturbance types, suggesting that environmental differences along plant successional gradients drive patterns in carabid assemblages. Furthermore, assemblage differences between older burned and clear-cut stands indicate that the type of disturbance influences long-term carabid recovery. Relationships between these findings and issues related to conservation of biodiversity and climate change are discussed.

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CHAPTER 1

General Introduction: Impacts of forestry, wildfire, and succession on epigaeic carabid assemblages in northern forests

1.1 Succession after natural and anthropogenic disturbance

Wildfire has long played an important role in structuring forest landscapes of North America by periodically re-setting successional processes when patches of stable, old-growth forests are burned (Landres et al. 1999). Forest succession drives changes in habitat available for various species (e.g., Whipple and Dix 1979) by providing a heterogeneous patchwork of stands that support high levels of biodiversity on the landscape (Bonan and Shugart 1989; Hansen et al. 1991; Rainio and Niemelä 2003; Thom and Seidl 2016). Therefore, persistence of wildfire and other natural disturbances on forest landscapes is necessary for maintenance of habitats to support the biodiversity that has evolved in the context of these processes.

The effects of wildfire vary depending on factors such as fire intensity and scale (Hutto 2008). High intensity fires, being more destructive, lead to increased mortality of ground dwelling fauna and flora, reduce availability of duff and coarse woody debris (CWD), and result in more exposed mineral soil (Wikars and Schimmel 2001; Keeley 2009). Conversely, lower intensity fires leave behind more duff and CWD and more surviving ground-dwelling organisms (Bond and Keeley 2005). The intensity of fire is highly dependent on factors such as weather and fuel quantity and quality (e.g., Thaxton and Platt 2006) that can vary widely from site to site. Higher intensity burns initiate more predictable successional patterns than do low intensity burns as degree of environmental change is directly proportional to fire intensity (Hutto 2008). Most significantly, burning opens up habitats to warming and drying, and leaves burned material and charcoal behind. These effects mark the beginning of decades-long succession that leads towards the regrowth of mature forests (Romme and Knight 1981).

The introduction of forestry and fire-suppression by humans in boreal and temperate forests have altered natural disturbance regimes in ways detrimental to many forest species (Spence et al. 1996; McCullough et al. 1998). Therefore, understanding how species react to natural and anthropogenic disturbances such as wildfire and harvest is essential for development of sustainable forest management practices to mitigate loss of biodiversity (Bergeron et al. 1999). Compared post-burn areas, managed areas have less mineral soil, coarse woody debris (CWD), and burned materials except for areas used for controlled burning of logging slash after harvesting (Corns and Roi 1976). Furthermore, after some harvests, there is heavy ground disturbance caused by machines and equipment and this greatly increases exposure and compaction of mineral soil and affects vegetation regeneration and community composition (Johnson et al. 1991; Bergstedt et al. 2008). Removal of biomass during clear-cut harvest and the opening of the canopy results in warming and drying of the ground, making way for early-successional vegetation such as grasses (Bergstedt et al. 2008). Such effects resemble those that follow high intensity burning; however, unlike high intensity burns, the seedbank in the topsoil is preserved after harvest, and plants that occupied the site before disturbance will regrow more quickly, so long as the topsoil is not moved (Paquin and Coderre 1997).

1.2 Carabidae as an indicator group

Epigaeic carabid beetles have been useful model organisms for studying impacts of ecosystem disturbance and recovery because their biology and taxonomy are relatively well-known, they respond to habitat change, and samples of local assemblages are easy to collect using standardized methods (Spence and Niemelä 1994). In addition, the composition and structure of forest carabid assemblages vary with both stand age and disturbance, and thus they been useful as a bioindicator taxon for these features (Dufrêne and Legendre 1997; Brumwell et al. 1998; Villa-Castillo and Wagner 2002; Larsen et al. 2003; Rainio and Niemelä 2003; Pearce and Venier 2006; Work et al. 2008).

Epigaeic carabid species show three main habitat associations that reflect forest succession on managed northern forest landscapes. Species may be classified as forest habitat generalists, open-habitat affiliated, and mature forest affiliated (e.g., Niemelä et al. 1993; Heliölä et al. 2001). Generalist species are found in all types of habitats within older and younger forests and are not adversely affected by harvesting (Niemelä et al. 1993). In contrast, open-habitat and mature forest species respond strongly to disturbance and are associated with earlier or later stages of succession, respectively (Niemelä et al. 1993). After both fire and harvest alike, carabid communities have shown the same general pattern of open-habitat species colonizing within the first few years post-disturbance, followed by mature forest species slowly increasing and replacing open habitat species through time (Buddle et al. 2006). However, specific patterns in epigaeic carabid community composition appear to differ between the two disturbance types depending on how ecosystems are physically affected by burning versus clear-cutting (Niwa and Peck 2002; Moretti et al. 2004; Moretti et al. 2006; Niemelä 1997; Niemelä et al. 2007). Irrespective of the type of disturbance that resets forest succession, the species and relative abundance of carabid beetles are affected; however, the assemblages show recovery through time, defined as a slow turnover of species concurrent with forest succession whereby assemblages increasingly come to resemble those typical of old-growth forests (i.e., returning to pre-disturbance composition and structure).

1.3 Impacts of wildfire on carabids

After high intensity fire, carabid assemblages tend to recover more slowly in initial phases compared to their recovery after clear-cut harvest (Richardson and Holliday 1982; Buddle et al. 2006). The carabid species that prosper in a regenerating pyrogenic stand must be well-adapted to open, dry habitats (Holliday 1991; Paquin and Coderre 1997; Niwa and Peck 2002). The species that depend most on fire are those that colonize soon after a fire, but a subset of these are not usually seen after harvesting. For example, some *Sericoda* species are described as pyrophilic, because they are associated with stands immediately after wildfire events (Lindroth 1961-69). On the other hand, low intensity fires leave more habitat refuges behind for forest species to persist, particularly when they occur in late-successional forests (Gandhi et al. 2001). Furthermore, because early successional open-habitats are necessary to maintain populations of many open-habitat species, disturbances such as windthrow and high intensity fires are still required on forested landscape (Hutto 2008). In the end, though some aspects of fire are replicated in clear-cut harvest, pyrophilic species such *S. quadripuntata* (DeGeer) and *S. bembidioides* Kirby are generally absent without burning (Koivula et al. 2006).

1.4 Impacts of clear-cut harvest on carabids

After clear-cutting an area, there is high activity of forest generalist carabid species, and activity of residual mature forest affiliated species that survived as eggs, larvae, and adults in topsoil or other refuges persists for the first few seasons following harvest. This results in higher species richness in early successional forests (Nguyen-Xuan et al. 2000; Gandhi et al. 2001; Saint-Germain et al. 2005). A few years after harvest, populations of these residual forest species begin to disappear, and open-habitat species become more numerous and diverse (Niemelä et al. 1993; Work et al. 2010). For example, many *Amara* and *Harpalus* species, which are seed-feeders (Kromp 1989), are caught at high rates in early successional stages. These organisms benefit from seeds provided by grasses, which colonize quickly after clear-cutting (Nilsson and Örlander 1999). In general, open-habitat species appear to establish sooner after clear-cutting than after burning (Buddle et al. 2006).

1.5 Long-term succession

Despite differences in initial carabid responses after disturbances caused by clear-cut harvest and wildfire, assemblages begin to more closely resemble those found in old-growth stands by around 30 years, though assemblages do not yet resemble those of old-growth stands (Buddle et al. 2006; Saint-Germain et al. 2005). At this point, assemblages include more forest species and fewer open-habitat species (Niemelä 2007; Pohl et al. 2007). Late-successional forests change much more slowly and have lower species richness than do early-successional forests, though there are more specialized species (Johansson et al. 2016). There is still much overlap in carabid species assemblages between medium aged (40-60 years) and old-growth (80-130 years) stands after clear-cutting, although more rare species that seem to be habitat specialists are found in older forests (e.g., Johansson et al. 2016; Venier et al. 2017). Thus, there are conservation concerns for species that depend on habitats of old-growth forests, especially on extensively harvested landscapes where stands may be re-cut before populations of such relatively rare species can re-establish themselves (Spence et al. 1996). It is still unclear how long it will take for forests regenerating from clear-cut harvest to re-establish species assemblages that are characteristic of uncut, mature forests.

My work builds on a previous study by Niemelä et al. (1993) on recovery of epigaeic carabid assemblages after clear-cut harvest in lodgepole pine forests near the town of Hinton, Alberta. The history of clear-cut harvesting in the Hinton area goes back to the mid-1950s, and the area includes some of the earliest clear-cuts in Alberta. Thus, further work in this area provides an opportunity to assess recovery of carabids more than 50 years after harvest, something that has not yet been done for any forest type in Alberta. Responses of epigaeic carabids so long after harvest have been assessed in other forest types and such studies have shown that recovery remains incomplete even 50 years after disturbance, particularly with respect to rare species of mature forest (e.g., Johansson et al. 2016; Venier et al. 2017). In 1989-90, Niemelä et al. (1993) used a chronosequence approach to compare carabid species assemblages from clear-cut stands 1-27 years post-harvest with assemblages from old-growth stands of pyrogenic origin. In this thesis, I aimed to assess how far carabid recovery had progressed 23-24 years later (in 2013-14) using data from a survey of clear-cut stands ranging across a chronosequence of 12-53 years post-harvest. In addition, I sampled stands regenerating after fires that occurred 17 and 58 years prior to sampling, supporting a comparison of assemblages between pyrogenic and harvested stands of similar age. Assemblages from harvested stands were compared against those from old-growth stands >100 years old, which were assumed to represent pre-harvest conditions, to assess progress toward recovery. Thus, my study provides insight about recovery of carabid species assemblages up to 53 years after clear-cutting in comparison to recovery 17 and 58 years after fire.

CHAPTER 2

Responses of ground beetle (Coleoptera: Carabidae) assemblages to clear-cut harvest and wildfire in lodgepole pine stands of western Alberta, Canada

2.1 Introduction

Periodic natural disturbances such as wildfire result in a mosaic of successional habitats on forest landscapes (Holliday 1991). Recovery from disturbance through forest succession has sustained variation in forest biodiversity that in part flows from adaptations of many species of plants and animals for conditions that occur only during certain stages of forest succession (Jonsson and Esseen 1990; Boulinier et al. 1998; Tews et al. 2004). However, in the past century, anthropogenic disturbance has altered the environmental background through increased commercial clear-cutting in many regions, resulting in unintended consequences for populations of sensitive species (e.g., Spence et al. 1996).

Understanding how forest harvest may qualitatively affect the biota and ecosystem functions in comparison to natural disturbances such as wildfire requires research that considers a substantial portion of the succession sequence (e.g., Buddle et al. 2000; 2006). Immediately following forest disturbance, changes associated with site recovery are highly dynamic for a few years, making it difficult to decipher trajectories of biodiversity responses over brief time frames. It appears to require a decade or more to clearly identify trajectories of faunal succession in northern forests, and much longer to be able to adequately determine whether assemblages are recovering towards a pre-disturbance structure characteristic of mature stands (Buddle et al. 2006; Venier et al. 2017).

Several studies in northern forests of North America have examined biodiversity responses to disturbance over more than five years post-disturbance, with most focused mainly on the recovery of plants and arthropods (e.g., Niemelä et al. 1993; Buddle et al. 2000; Buddle et al. 2006; Hart and Chen 2006; Johansson et al. 2016; Venier et al. 2017). Carabid beetles have been frequently chosen as model arthropods for such research as they are diverse, taxonomically well known, easily sampled in a standardized way, and there is a large body of ecological literature making them well-understood compared to many other invertebrate groups (Rainio and

Niemelä 2003; Niemelä et al. 2007). Furthermore, carabids are present and sensitive to a broad range of forest disturbances because most may alter but do not remove the ground surface habitats that they depend on. Thus, changes in beetle assemblages can provide insight about responses to forest harvest across a full gradient of disturbance (e.g., Work et al. 2004).

In a medium-term study of arthropod responses to forestry in North America, Niemelä et al. (1993) used a chronosequence approach in Cordilleran forests of west-central Alberta to study carabid species assemblages of clear-cut stands aged 1-27 years post-harvest. Although the assemblages seemed to be recovering toward the structure of those found in old unharvested stands aged 80-100 years, recovery was at best incomplete in harvested stands. They also noted that stands that were clear-cut harvested <15 years previously supported many open habitat carabid species and lacked mature forest species. The work prompted concern about conservation of species associated with old-growth forest because a number of mature forest species had not reappeared in stands by 27 years after harvest, and surrounding forests that could serve as sources of these beetles continued to be harvested rapidly (Niemelä et al. 1993; Spence et al. 1996; Pohl et al. 2007).

Other studies about responses of epigaeic arthropods to forest disturbance have been conducted in various forest types across Canada (e.g., Buddle et al. 2006; Koivula and Spence 2006; Cobb et al. 2007; Venier et al. 2017). These have identified several relatively consistent patterns in arthropod recovery following natural and anthropogenic disturbances, especially in the early stages of succession. For example, immediately following forest disturbance, there is generally high species richness consisting of both habitat generalist species and species with affinity to open habitats, in addition to dwindling populations of species affiliated with mature forest that persist only for a few seasons following harvest (e.g., Niemelä et al. 1993; Gandhi et al. 2001; Buddle et al. 2005; Saint-Germain et al. 2005). After several decades, mature forest species begin to re-establish as the open-habitat species disappear with canopy closure and assemblages like those seen before disturbance begin to reappear (Buddle et al. 2006; Johansson et al. 2016; Venier et al. 2017).

Type of disturbance affects recovery of carabid assemblages, and several studies (e.g., Buddle et al. 2006, Cobb et al. 2007) suggest that recovery differs more drastically between clear-cut and burned stands in the first decade after disturbance. This can be attributed to fundamental differences in habitat conditions following wildfire and harvest such as: increased exposure to mineral soil, amount of charred material, and overall amount of dead wood commonly seen after high-intensity burning (Cobb et al. 2007). Therefore, carabid assemblages recover along different trajectories after burning or harvest but show signs of convergence around 30 years after disturbance in aspen-dominated boreal mixedwood (Buddle et al. 2006). Fewer studies have addressed recovery in later stages of forest succession (e.g., Gobbi et al. 2006). There is some evidence that species assemblages begin to resemble those of coniferous-dominated old-growth stands after roughly 40 years of succession (e.g., Johansson et al. 2016; Venier et al. 2017). However, it remains uncertain whether communities recover completely to pre-harvest condition, and if so, how long it takes. Given clear variation in trajectories of recovery depending on disturbance intensity, forest type, and location, it is unlikely that answers can be generalized across forest types (Reich et al. 2001).

In this thesis, I have studied carabid assemblages in lodgepole pine-dominated forests near Hinton, Alberta, including some of the stands also studied by Niemelä et al. (1993). I explored how carabid assemblages have changed given additional time for recovery. I included stands, harvested subsequent to the Niemelä et al. (1993) study, to test the generality of the responses they observed in a more recent chronosequence in stands ranging from 12 to 53 years post-harvest. In addition, I compared the assemblages in two stands that burned 17 and 58 years before my study with those in stands of similar age disturbed by logging. Finally, samples of assemblages from pyrogenic mature stands aged 104-114 years old were used to provide a reference condition to assess post-disturbance recovery of the fauna. Thus, faunal recovery, in terms of assemblage composition, is viewed as incorporating three processes: retention of populations of generalist species after disturbance, disappearance of open habitat species, and recolonization by mature forest species.

Using data outlined above, I tested three main hypotheses about carabid assemblage succession in lodgepole pine forests disturbance. First, by further sampling stands examined by Niemelä et al (1993), I tested whether carabid assemblages continued to show recovery after clear-cutting over the intervening 23-24 years, and predicted that assemblages in the oldest clear-cuts sampled in 2013-14 would be more similar to those of unharvested controls than were the oldest clear-cuts sampled in 1989-90. Second, by comparing fauna of harvested stands of similar age across the two studies, I tested whether recovery rate was consistent irrespective of time period, and predicted no difference in recovery rate. Third, by comparing fauna of 17- and 58-year-old burned stands to harvested stands of similar age, I tested whether faunal recovery was similar irrespective of disturbance type. Based on findings of Buddle et al. (2006), I predicted that the youngest burned and harvested stands would have divergent faunas but that the successional trajectories would converge so that faunas in the oldest burned and harvested age class would be more similar to each other. In addition, by examining correlations between plant and mineral soil cover and carabid assemblages (e.g., Siemann et al. 1999), I sought to determine whether plant and soil variables may be used to predict carabid assemblages and post-disturbance recovery.

2.2 Methods

2.2.1 Study area

This study was conducted in a ca. 160 km^2 area of the eastern foothills of the Rocky Mountains, 18-23 km south of Hinton, Alberta (53°22'13"N, 117°38'12"W, see Figure 1). This area has the longest history of continuous commercial forestry in Alberta, dating back to 1955, and includes two areas recovering from wildfires, the 8000 ha 'Gregg River Fire' that burned in 1956 (53°14'24"N, 117°20'23"W) and the 3000 ha 'Christmas Fire' that burned in 1997 (53°12'4"N, 117°27'2"W) (Udell et al. 2002).

The work was conducted in stands comprising mainly *Labrador tea–mesic* and *tall bilberry/arnica* ecosites (Beckingham et al. 1996) that are common in in the Upper Foothills Natural Subregion. Mature stands of these two ecosites harbour similar carabid assemblages (D. Langor, unpublished data). Regenerating and control stands were largely coniferous, dominated by lodgepole pine, *Pinus contorta* Douglas var. *latifolia*, and white spruce, *Picea glauca* Moench. The dominant shrubs included species of *Alnus* and *Salix*, which in 2013-14 were found mainly in younger stands (up to 20 years old) with more open canopies. Dominant ground vegetation cover also varied with stand age. Older stands had more bryophytes and younger stands had more forbs and graminoids.

2.2.2 Stands studied

Carabid assemblages were sampled in stands that differed in age and disturbance history (see Table 1 for stand characteristics). The analysis here considers data from two periods: 1989-90, as part of the dataset developed and analyzed by Niemelä et al. (1993), and 2013-14 (collected and analyzed as described herein). Five post-harvest age classes of harvested stands were sampled in 2013-14: 10-13 years (designated H12 to represent the mean age in 2013), 18-20 years (H19), 29-36 years (H33), 39-45 years (H42), and 52-54 years (H53). In addition, two areas burned by wildfires in 1956 (F58) and 1997 (F17) and unharvested pyrogenic-origin ’control’ stands aged 104-114 years (F110) were also sampled. Three replicates of each harvest and fire age class were sampled during 2013-14. Two of the replicates of each of the H33, H42, H53, and F110 stands had also been previously and similarly sampled in 1989-90 when their ages were, respectively, 5-12 years (designated H9), 15-21 years (H18), 28-30 years (H29), and 80-90 years old (F85).

2.2.3 Beetle sampling and identification

Carabid assemblages were sampled using pitfall traps of the general design described by Spence and Niemelä (1994) and used by Niemelä et al. (1993). Each trap consisted of two parts: 1) a ‘sleeve’ (1L plastic yogurt container, 10-cm in diameter with perforations in the bottom to allow drainage) imbedded in the soil with the upper lip flush to the ground, and 2) an inner removable ‘trapping cup’ (0.5L plastic yogurt container). The inner cup contained ca. 150 mL of low-toxicity propylene glycol (ethylene glycol in 1989-90) that served as a killing agent and preservative. Each trap was shielded by an elevated plastic lid (wooden lids were used in 1989-90) to exclude precipitation and debris.

Six traps were deployed per stand during 1989-90, but this was increased to eight traps in 2013-14 in hope of offsetting losses anticipated from trap disturbance by mammals. During both periods, replicate stands were located at least 500 m from each other (except for two of the H12 stands which were separated by a road and were 60 m apart) to minimize spatial autocorrelation, which appears to be minor in northern forests (Blanchet et al. 2013). Most traps within stands were separated by at least 40 m during both sampling periods to ensure that trapping transects covered a large portion of each stand. In four smaller stands, H42 (replicate 1), H42 (2), F17 (2), and H12 (1) (See Figure 1), this spacing was not possible because of stand size, so distance between traps was reduced to no less than 15 m, a distance thought to be sufficient to ensure sample independence (Digweed et al. 1995). In addition, most traps were placed at least 50 m from the stand or cut-block edge to avoid possible edge effects (Spence et al. 1996); however, because of stand shape and size, 2-3 traps in each of stands H33 (2), H41 (2), and F17 (2) were 15-20 m from the nearest forest edge, a distance believed sufficient to minimize edge effects (e.g., Spence et al. 1996; Phillips et al. 2006; Pohl et al. 2007).

Sampling during both study periods was conducted from May to early September, i.e., encompassing the frost-free season, totaling 100-110 sampling days in each year. Traps were placed in the exact same locations for both years of each period, except for the H12 (1) and H12 (2) stands that were sampled only in 2014. Replicates of this age category from 2013 were subsequently deemed to be physically too far away (c. 15 km) from the others of the study and were abandoned in 2014 in favour of closer stands. Beetles were collected and traps were replenished with preservative at approximately bi-weekly intervals. Catches were returned to the laboratory for sorting and preservation in 75% ethanol. All carabid specimens were counted and identified to species using keys (e.g., Lindroth 1961-69) and reference material deposited in the Strickland Entomology Museum and Northern Forestry Centre. Nomenclature follows Bousquet et al. (2013).

2.2.4 Vegetation and soil variables

Data about cover of ground vegetation, amount of exposed mineral soil, and tree basal area were recorded around each trap deployed in 2013-14 and then averaged across the eight traps in each stand to calculate a stand mean used in analyses.

Plant and mineral soil cover. Percent cover in the combined herb and ground layers was estimated for all plant species comprising ≥ 5% cover in 1 m^2 quadrats near each trap. In order to minimize the effect of trap disturbance when assessing the vegetation, vegetation quadrats were consistently placed 2 m to the north of each trap, in areas representative of the trap's immediate environment. Mineral soil cover was estimated alongside vegetation cover within these same quadrats. Forbs were identified to species using keys in Royer and Dickinson (2007). Bryophytes and graminoids were not determined to species, but percent cover was determined for these broad categories.

Trees. Trees were counted in prism plots (PRF = 3) centered immediately above the trap (Bruce 1955), and each tree tallied in the prism sweep was identified to species. Proportion of overall tree basal area represented by each species in the prism plot was calculated around each trap. In addition, a convex spherical densitometer (Model-A, manufactured by Forestry Suppliers, Jackson USA) was used to measure canopy cover over each trap (Strickler 1959).

2.2.5 Weather condition data

Temperature and precipitation data during the 1989-90 and 2013-14 field seasons (May to September), recorded by Alberta Climate Information Service (ACIS), was averaged for each collection period. The data representing township T049R24W5 (region of sample area, south of Hinton) were estimated by interpolating data from the eight nearest weather stations (ACIS 2016). Change in temperature and precipitation data from 1989-90 to 2013-14 was also calculated. Temperature change was determined by comparing average daily maximum and minimum temperatures (°C) between each sample period while precipitation was assessed by determining the % change in total accumulated rainfall between the two sample periods. It was predicted that there would be a warming and drying of weather conditions from 1989-90 to 2013-14 that could reflect climate change effects in the area. Table A of the Appendix summarizes monthly and mean daily temperatures for each month during both collection periods.

2.2.6 Statistical analyses

Sampling effort for carabids varied across stands, sample periods, and successive years, reflecting occasional trap disturbance by wildlife, the sampling of two H12 stands only in 2014, variation in trap-days among field seasons, and the different numbers of traps used per stand in 1989-90 versus 2013-14. Thus, data for each stand and sample period were standardized to number of individuals caught per 1000 trap-days (roughly the number of trap-days per stand per year in 2013 and 2014). A trap-day is defined as one trap operating for one day. These measures of standardized catch were compared using Analysis of Variance as implemented in R (RC Team 2016) with $\alpha = 0.05$.

Carabid species richness, however, was calculated based on unstandardized catch data pooled for each ‘stand age × disturbance type’ combination using coverage-based rarefaction (Chao and Jost 2012). Coverage-based rarefaction estimates total species richness based on the “completeness” of a sample (i.e., coverage), rather than limiting comparisons based on the lowest sample size (as with a traditional, individual-based rarefaction). Extrapolated species richness and the 95% confidence interval for each ‘stand age × disturbance type’ combination is derived from 100 randomizations with total species richness set at twice that observed (Chao and Jost 2012). Since coverage-based rarefaction considers both species richness and catch rate (‘activity-abundance’), estimates can be fairly interpreted as a diversity index (e.g., Buddle et al. 2005). Rarefactions were calculated using the iNEXT package in R (Hsieh et al. 2016; RC Team 2016).

Composition of carabid assemblages was compared among ‘stand age × disturbance type’ combinations and sampling periods using unconstrained principal component analysis (PCA) based on standardized catch of each species pooled within each stand, as described above. First, basic relationships among assemblages recovering after harvest were established in an initial PCA calculated using data from only the harvested age classes collected during both sample periods. The species loadings from this PCA model were then used to estimate the coordinates for burned stands from 2013-14 and all control stands using trap catches from both sampling periods. The resulting ordination depicts the relative positions of all stands in ordination space in relation to the best-fit configuration of harvested stands, supporting clear understanding of both fire effects and extent of recovery.

A constrained redundancy analysis (RDA) was applied to data from 2013-14, including both burned and harvested stands, to determine the extent to which vegetation variables corelated with carabid assemblage composition. Data about ground vegetation cover, mineral soil cover, and tree basal area, as described above, were included in the RDA as possible explanatory variables. Position of all stands was included on each RDA plot and 95% confidence intervals were calculated for each ‘stand age × disturbance type’ combination. Statistically significant vegetation variables were included in the RDA plot as vectors that describe the strength (vector length) and influence (vector direction) of their effects on the assemblages. Both PCA and RDA ordinations were calculated using the ‘vegan’ package in R (Oksanen et al. 2013; RC Team 2016). Standardized carabid catches for each stand were transformed to Hellinger distances before analysis to reduce the effect of dominant species on the resulting ordinations. Estimates of each of the ‘stand age × disturbance type’ combinations for which 95% confidence intervals do not overlap in the RDA are considered to differ significantly.

To illustrate habitat affinity of individual taxa represented by 15 or more individuals in the 2013-14 data set, histograms were plotted showing the proportions of overall standardized catch for each ‘stand age × disturbance type’ combination. Most taxa were treated at the species level, but *Amara*, *Harpalus*, and *Notiophilus* were included at the genus level to increase sample sizes, given that congeneric species have similar general habitat requirements and exhibit similar responses to disturbance. Proportion of standardized catch was calculated by dividing the sum of standardized catch for all stands within ‘stand age × disturbance type’ combinations by the sum of standardized catch for all stands. To assess if the presence of a taxon in a group of stands was significant, standardized catch rate was compared against the expected catch rate, based on proportion of sampling effort. Proportion of sampling effort was calculated by dividing total number of trapping days per ‘stand age × disturbance type’ combination by the sum of trapping days for all stands (Table 1). Habitat affinity of each taxon was then estimated based on whether relative standardized catch between younger (H12, F17, H19, and H33) and older (H42, H53, F58, and F110) stands was higher or lower than expected. Catch of generalist taxa were not expected to vary between young or old stands whereas taxa with affinity for open habitats were expected to predominate in younger stands and mature forest affiliated taxa were expected to be more likely trapped in older stands.

A chi-squared goodness of fit test was calculated for common taxa, using raw catch data to assess if the distribution of each taxon was statistically similar across all ‘stand age × disturbance type’ combinations. Observed raw catch data was compared against expected catch (based on proportion of sampling effort, explained above) to obtain a chi-squared goodness of fit statistic (χ^2 with significance defined as $p<0.05$).

2.3 Results

2.3.1 Catch and species richness

A total of 5635 ground beetles comprising 44 native species was captured during 2013-14

(Table 2). Of these, *Calathus advena* (LeConte) and *Calathus ingratus* Dejean were the most abundant, comprising 34% and 28% of total catch, respectively. Nine species were represented by only one or two specimens and 14 other species by <15 individuals. Most species were caught during both years, and the fifteen species caught in only one year were all relatively uncommon (1-28 individuals, see Table 2). Eight species caught in 1989-90 were not caught in 2013-14: *Agonum quinquepunctatum* Motschulsky, *Amara apricaria* (Paykull), *Amara pseudobrunnea* Lindroth, *Harpalus innocuus* LeConte, *Harpalus nigritarsis* Sahlberg, *Nebria crassicornis* Van Dyke, *Notiophilus aquaticus* (L.), and *Notiophilus simulator* Fall (all of these species were rare in 1989-90 with fewer than 5 individuals caught). Also, fourteen species caught in 2013-2014 were not trapped in 1989-90 (Table 2).

In a two-way ANOVA including only harvested and burned stands of similar age in 2013-14 (i.e., H19 and F17; H53 and F58), overall standardized catch rate of carabids differed significantly between stand ages ($F_{1,5} = 6.2$, $p = 0.038$), but not disturbance types ($F_{1,5} = 0.5$, $p = 0.82$). In a one-way ANOVA of catches from all harvested age classes and the F110 stands sampled in 2013-14, stand age also significantly affected carabid catch rate ($F_{5,17} = 11.9$, $p < 0.01$). Post-hoc Tukey's tests showed that the mean standardized catch of beetles was significantly higher in H12 than in H19, H33, H42, and F110 but not H53 (Table 1). Mean overall catch rate in the F110 stands were among the lowest, but differed statistically only from that in H53 and H12 stands. Catch rate did not differ significantly among H19, H33, H42, and H53 transects, indicating a consistent reduction in carabid catch rate in stands older than 12 years of age. In addition, a one-way ANOVA including all pyrogenic stand age classes (F17, F58, and F110) showed no statistically significant differences in catch rate based on age ($F_{1,8} = 1.4$, $p = 0.28$); the lack of a trend likely reflects high variability in high catch rate among the H58 stands.

Rarefaction-estimated carabid species richness for all 'stand age × disturbance type' combinations was obtained from the 2013-14 data, with the lowest maximum coverage value being 97.9% (F17). Differences were considered significant if 95% confidence intervals did not overlap. In general, richness was highest in the youngest harvested stands (H12, H19) but dropped to lower levels in H33 stands before increasing again in the middle-aged stands (H42 and H53). A similar trend was evident for the burned stands, i.e., species richness was high in the youngest stands (F17), dropped significantly in the F58 stands, and was higher again in the oldest stands (F110).

2.3.2 Assemblage structure

Analysis of carabid assemblage structure using unconstrained PCA resulted in a model (Figure 2) explaining 43.1% of total variance in the data collected in both 1989-90 and 2013-14 from harvested stands. Of the constrained variance, 41.9% and 15.6% could be respectively attributed to axes 1 and 2. A PERMANOVA applied to the same data used to construct the PCA model was statistically significant ($F_{7,13} = 4.6$, $p = 0.001$, adj-$R^2 = 0.71$).

The chronosequence was generally reflected in the PCA ordination, with stand age increasing from left to right (Figure 2). Data from 2013-14 documents recovery of both burned and harvested stands toward the target defined by the pyrogenic controls (F110) that represents the assumed pre-disturbance condition. However, the ordination suggests that carabid assemblages recovered more quickly or were less affected by disturbance (i.e. some mature species survived disturbance) in burned stands than in harvested stands, and this trend was evident as early as ca. two decades post-disturbance (Figure 2 – compare H19 to F17). By 50-60 years post-disturbance, assemblages in burned stands (F58) and harvested stands (H53) had converged towards those characteristic of control stands (F110), and assemblages from F58 stands were essentially indistinguishable from that in one of the F110 stands.

Comparison of harvested stands of similar age between sampling periods shows that assemblages sampled early in post-harvest recovery, i.e., H9 in 1989-90 and H12 in 2013-14, were indistinguishable, suggesting that the regional composition of these early post-harvest assemblages was similar irrespective of time period. However, assemblages in H18 and H29 stands sampled in 1989-90 differed markedly from similarly aged H19 and H33 stands, respectively, in 2013-14, with the stands sampled in 2013-14 more similar to unharvested controls. This suggests that carabid assemblages recovered faster in these age classes of harvested stands in 1989-90 compared to 2013-14. Assemblages in the two mature pyrogenic stands (F85) sampled in 1989-90 did not change much after 23 years (compare to the two most similar F110 stands in Figure 2), but the other F110 stand added in 2013-14 (the one furthest to the right in Figure 2) harbored an assemblage that differed markedly from the others.

Redundancy analysis (RDA) applied to 2013-14 data underscored significant differences in assemblage composition among ‘stand age × disturbance type’ combinations (ANOVA: $F_{7,16} = 4.74$, $p = 0.001$, adj-$R^2 = 0.72$), corroborating patterns revealed in the PCA. Carabid assemblages in stands originating from fire and harvest changed over time toward assemblage composition typical of mature stands; however, those from the older burned stands (F58) were indistinguishable from those of control stands while those in similarly aged clear-cut stands (H53) differed from those of controls. Vegetation variables statistically explained 37.5% of the variance in the original beetle catch data and accounted for 34.4% of the variance in the constrained model. Twelve variables – nine related to percent cover by ground vegetation or exposed mineral soil, and two reflecting basal area of white spruce (*Picea glauca* Moench) and mountain alder (*Alnus crispa* Chaix) – accounted for most of the constrained variance in species composition of assemblages (Table 3). Data about canopy cover, however, did not significantly corelate with any of the variation in beetle assemblages. The following trends can be observed in the RDA (Figure 3):

1) Carabid assemblages of the youngest harvested stands (H12 and H19) clustered furthest away from those in the F110 stands. Vegetation variables closely correlated with H12 carabid assemblages included percent ground cover by graminoids, white spruce (*Picea glauca* Moench) saplings, cream pea (*Lathyrus ochroleucus* Hook), dandelion (*Taraxacum officinale* L.), and wild strawberry (*Fragaria virginiana* Duchesne). Percent ground cover by fireweed (*Chamaenerion angustifolium* L.) and wild blueberry (*Vaccinium virgatum* Aiton) and basal area of mountain alder (*Alnus crispa* Chaix) were associated with the structure of H19 carabid assemblages. Carabid assemblages of the youngest burned stands, F17, overlapped with those of H19 but were markedly closer to target assemblages of the F110 stands.

2) The carabid assemblages of middle-aged regenerating stands (H33, H42, and H53) clustered together and were closely associated with high percent cover of bunchberry (*Cornus canadensis* L.). They clustered near the oldest burned stands (F110), suggesting succession of carabid assemblages towards the structure characteristic of mature stands. Variability was highest among H33 stands and decreased in older harvested classes.

3) Carabid assemblages in the oldest pyrogenic stands (F58 and F110) were most

strongly correlated with high ground cover of bryophytes and basal area of white spruce (*Picea glauca*). Assemblages of mature pyrogenic stands (F110) were the most variable of any age group of stands in the RDA (largest 95% confidence interval); however, the variation of carabid assemblages in F58 stands was fully contained in the confidence ellipse for F110 stands. Mineral soil cover is also correlated with assemblages of the oldest pyrogenic stands.

4) Despite evidence of recovery in both harvested and burned stands, 95% confidence intervals for carabid assemblages in stands of similar age but different disturbance history (F17 and H19; F58 and H53) did not overlap, underscoring that the recovery trajectories of assemblages differed between the two disturbance types.

2.3.3 Possible influences of climate

Weather condition data from ACIS including mean daily and monthly, maximum and minimum temperatures and mean monthly accumulated precipitation for the field seasons (May-September) during 1989-90 and 2013-14 is summarized in Table 4. Although mean daily minimum daily temperatures were similar between the two collection periods (<0.5 °C cooler in 2013-14), mean daily maximum temperatures were 1.9 °C warmer and mean precipitation was nearly 33% lower in 2013-14. This suggests that conditions were hotter and drier in 2013-14, on average. Temperature data were also more variable during the 2013-14 field seasons with larger monthly minimum and maximum temperature extremes.

2.3.4 Responses of individual species

No commonly collected carabid taxon (i.e., those with >15 individuals caught) was evenly distributed among ‘stand age × disturbance type’ combinations according to expected catch based on trapping effort (i.e., χ^2 tests were significant at $p < 0.001$ for all taxa; Figures 4-6). Carabid species sampled in 2013-14 showed one of three general patterns of response to harvest and wildfire, as originally identified by Niemelä et al. (1993). Forest generalist species were not adversely affected by disturbances and were commonly found in stands representing the full range of age classes and disturbance types, although they were more common in some than others. Open-habitat species showed strong affinity for younger disturbed stands that had not yet reached canopy closure and that retained patches of exposed mineral soil. Mature forest species showed strong affinity to interior habitats characteristic of mature stands and were adversely affected by disturbance.

2.3.4.1 Forest generalist species

Calathus ingratus and *Stereocerus haematopus* (Dejean) were relatively common across all forest age classes and both disturbance types (Figure 4). However, almost half of all *C. ingratus* specimens (roughly twice as many as expected) were collected in the two oldest harvested age classes, H42 and H53, while 10% of the overall catch was collected in 58-year-old burned stands (close to that expected). Thus, wildfire is not necessary for recovery of populations of this species, but populations were especially promoted by conditions prevailing in stands 4-5 decades after harvest. *Stereocerus haematopus* occurred in all age classes of forest, but >80% of catch was collected in H42 or older stands (expected proportion was 54%), with about half of them found in F58 and F110 stands. Niemelä et al. (1993) also observed that *C. ingratus* and *S. haematopus* were present in all ‘stand age × disturbance type’ combinations.

With the addition of older regenerating stands (H42, H53) to the chronosequence in 2013-14, several taxa that showed affinity with open-habitats in 1989-90 appeared to be more evidently forest generalists in 2013-14. For example, *Notiophilus* spp. were considered open habitat specialists in 1989-90 but were found in nearly all age classes of regenerating clear-cut stands in 2013-14 (but not in H12), with 75% of standardized catch from H53 stands. However, this interpretation must be offered with caution because most individuals were caught from a single replicate H53(2). This stand could have simply been somehow more suitable to *Notiophilus* (e.g., presence of favourable microhabitat unrelated to age) as many individuals, mainly of *N. borealis* Harris and *N. directus* Casey, were also caught from a single trap. Nonetheless, the vegetation composition, mineral soil, or tree basal area around this trap had no notable characteristics. However, even excluding this stand, it is clear that *Notiophilus* does not have strong affinity for the most open stands. *Patrobus foveocollis* (Eschscholtz) was disproportionately captured in open habitats during1989-90 but was more evenly distributed across the ‘stand age × disturbance type’ combinations in 2013-14. However, the majority of *P. foveocollis* specimens were caught from two stands, H19(2) and H53(1) suggesting, as for *Notiophilus*, effect of some localized habitat feature not strongly correlated with stand age.

Some species apparently affiliated with mature forests based on inference from the 1989-90 data were more generally distributed among stand age classes in 2013-14. This is especially apparent for *Trechus chalybeus* Dejean which was found in every 'stand age × disturbance type' combination, albeit more commonly in harvested stands. *Pterostichus riparius* (Dejean) was also found in most harvested stands but the large majority were found in H53 stands, although all specimens in this age class were found in a single stand, H53(3), again suggesting localized favourable conditions. This species was rare in pyrogenic stands (one specimen in F110). *Scaphinotus marginatus* (Fischer von Waldheim) was rarely collected in the youngest harvested stands (H12, H19) but was more common in older age classes. This species may be a valuable indicator of recovery of carabid assemblages.

2.3.4.2 Open habitat species

A large group of 10 analyzed taxa, consisting of 23 species (more than half of all species caught), was found exclusively or predominantly in young regenerating stands (H12, H19, F17), which typically have open canopies (Figure 5). Most of these taxa had their highest standardized catch in H12, with the exception of *Agonum placidum* (Say), *Miscodera arctica* (Paykull) and *Syntomus americanus* (Dejean), for which the highest standardized catches occurred in H19 or F17 stands. Of these three species, catches of only *M. arctica* were distributed unevenly among replicate stands across 'stand age × disturbance type' combinations, with two thirds of total catch from H19(2). Most taxa classified as open habitat specialists based on 2013-14 data were also similarly classified in 1989-90 (Niemelä et al. 1993). Notably, one species, *Trichocellus cognatus* (Gyllenhal), that was a common open habitat species in 1989-90 (139 specimens) was represented only by one specimen in 2013-14. Unlike all other open-habitat taxa which were trapped in several or most 'stand age × disturbance type' combinations, all 136 sampled specimens of *Agonum cupreum* Dejean were found only in H12 stands, mainly (>95%) from H12(1) and H12(3).

2.3.4.3 Mature forest species

No species commonly collected in 2013-14 was identified only or mainly from mature pyrogenic stands, unlike in 1989-90 when several species showed strong affinity for mature forests. However, *C. advena* and *Leistus ferruginosus* Mannerheim showed affinity for the two oldest age classes of pyrogenic stands (F58, F110) and for the oldest harvested stands (F53) (Figure 6). Considering that H53 and F58 stands are approaching maturity and have closed canopies, then these two species may be reasonably considered as mature forest specialists. Certainly, in 1989-90, when no regenerating stands over 29 years of age were available for study in the region, both species were classified as mature forest specialists. Thus, populations of many species with strong affinity for mature forests in 1989-90 showed recovery in the oldest post-harvest stands in 2013-14, including re-appearance in some of the stands where they were not captured 23-24 years earlier. Thus, it seems that > 29 years are needed for populations of these species to re-establish themselves in regenerating stands. These two species may thus be important indicators of stand recovery. Another species, *Carabus chamissonis* Fischer von Waldheim, showed notable affinity for mature stands in 1989-90; however, only eight specimens were collected in 2013-14, and this was insufficient to meet the criterion of ‘common species’. However, most specimens were collected in F110 stands, a finding that supports earlier indications that this is a mature forest specialist. The low numbers collected in 2013-14 may indicate that there has been a reduction in regional populations of this species over time.

2.4 Discussion

2.4.1 Carabid succession

This study provides a multi-decadal comparison of carabid responses to fire and harvesting in Cordilleran forests that extends earlier work (1989-90) in the same area (Niemelä et al. 1993). The study is also complimentary to other nearby work in the boreal mixedwood of Alberta (Buddle et al. 2006) as well as in other forest types elsewhere (e.g., Venier et al. 2017). Results from the 2013-14 chronosequence suggest that carabid assemblages in regenerating stands move increasingly with age toward their pre-disturbance structure, with middle-aged harvested stands (H33, H42, H53) more closely resembling undisturbed old-growth stands (F110) than young harvested stands (H12, H19). Overall carabid catch rate and species richness was highest in the youngest harvested stands (H12), reflecting mainly the high activity of diverse common open-habitat and forest generalist species. Thus, it is mainly the open habitat species that make the H12 assemblage markedly distinct from other ‘stand age × disturbance type’ combinations. Open-habitat species quickly disappear from the next oldest group of stands

(H19). This observation is consistent with other studies, underscoring the relatively short time frame for presence and activity of open-habitat species during early stages of forest succession (Holliday 1991; Buddle et al. 2006; Niemela et al. 2007; Johansson et al. 2016).

My results show that assemblages in the next youngest group of clear-cut stands (H19) show signs of recovery towards those of the presumed pre-harvest condition, mainly due to disappearance and decreased population levels of open habitat species; however, they were distinct from assemblages in the next oldest harvested stands (H33). Clearly, regional persistence of these open-habitat species depends on dispersal by flight, a common pattern in Carabidae (e.g., Turin and den Boer 1988), and thus regional persistence of such species depends on continued presence of young stands within an area constrained by adult flight ability.

Assemblages in middle-age stands (H33, H42 and H53) were similar to each other, showing much overlap in composition (Figure 3). Thus, it appears that forest conditions begin to stabilize with canopy closure. Carabid assemblages appear to change more slowly in these younger forests, but in this study, they remained distinct from those of the mature pyrogenic stands (F110). In contrast, assemblages of the F58 burned stands cannot be distinguished from the oldest pyrogenic stands. Thus, there is insufficient evidence that harvested stands will eventually recover even though their structure seems to be converging with that observed in the mature stands. At least, more time is required before assemblages meet the target compositions defined by pre-harvest conditions. Despite similar trends in species richness and catch rates, details about assemblage structure differed between harvest and wildfire as regenerating stands aged. Thus, although this data from stands regenerating after harvest suggests convergence toward the structure of mature pyrogenic stands, this pattern should not be extrapolated a century into the future given the uncertainties of climate change.

During both periods of study considered here, carabid assemblages showed evidence of recovery in harvested stands. Nonetheless, there appears to be differences in rate of recovery between 1989-90 and 2013-14. Assemblages from the H18 and H29 stands, as sampled in 1989-90, appear to be further from pre-disturbance levels than are those in stands of comparable age (H19 and H33, respectively) as sampled in 2013-14. Although some of the variation among similar age classes across sample periods may be driven by chance variation in microhabitats (e.g., Niemelä et al. 1996), the variation reflecting apparent differences in rate of assemblage change toward the target may be related to climatic differences among the two sample periods. Furthermore, assemblages of undisturbed mature stands remained relatively consistent between the sampling. Thus, if changing climate did indeed play a role in influencing the differences in younger age classes sampled 23 years apart, then assemblages of mature stands have shown greater resilience to change.

Temperature and moisture influence many aspects of an organism's life history including phenology, dispersal, and development, all of which are known to have implications for carabid population performance (Saska and Honek 2003; Venn 2016; Pozsgai et al. 2018; Tseng et al. 2018). For instance, when temperature and moisture conditions favour reproduction of a species, one expects higher catch rates. Likewise, aspects of climate have the potential to affect phenology and distribution of many plant and animal species, which could result in fundamental changes to entire ecosystems (Parmesan 2006). Therefore, the apparently faster recovery of carabid assemblages observed in harvested stands during 2013-14 compared to 1989-90 may be a result of climatic differences between the two collection periods, whether or not these reflect steady ongoing changes in climate. Nonetheless, ecosystems at higher elevations seem to be more sensitive to a warming climate (Dirnböck et al. 2011) and thus effects may be amplified in the relatively high elevation areas of the foothills around Hinton.

Some evidence for climate effects is provided by data for *T. cognatus*. The catch rate of this species was dramatically (>99%) lower during 2013-14 than in 1989-90 (Neimelä et al. 1993). Since *T. cognatus* was found mostly in younger regenerating stands in 1989-90, one would have expected it to be favoured by widespread logging in the Hinton area. However, this widespread boreal species is generally more common in northern areas and favours moist habitats (Lindroth 1961-69). Thus, it may be less able to sustain population near Hinton under a warming and drying climate. Data about weather during these two periods provides some support for this suspicion. Although the average daily minimum temperatures over the five frost-free months were lower in 2013-14, the average daily maximums were 1.9 °C warmer. Furthermore, average precipitation in 2013-14 was nearly 33% less than in 1989-90. Therefore, despite more variable temperature extremes during period two, the climate was both hotter and drier on average in 2013-14. More sampling is required to verify if this species has effectively disappeared or if climatic conditions of 2013-14 were anomalies. No other species displayed as dramatic a change in catch rate between 1989-90 and 2013-14.

2.4.2 Effects of disturbance type: wildfire vs. clear-cut harvest

Despite general large-scale similarities between harvest and wildfire in trajectory of change in carabid assemblages, there were notable differences, especially during early stages of succession. In ordinations, the carabid assemblages in F17 stands were much closer to the old-growth F110 stands (with some overlap) than to the similarly aged H19 stands. This contrasts with other studies from boreal forests that have noted delays in recolonization of some carabid species after burns as compared to harvest in younger stands (<10 years), attributing it to the immediate harsh effects of fire (Holiday 1991; Wikars and Schimmel 2001; Buddle et al. 2006). Of course, fire severity may influence rates of recovery, but there are no data available to compare fire severity among studies. Another notable difference between young burned and clear-cut stands is illustrated by the presence of *A. placidum*, *Carabus taedatus* Fabricius von Waldheim, and *S. americanus* in the F17 stands in much higher proportions than found in H19 stands. This likely reflects drier conditions in the post-burn stands, as these species are all xerophilic (Lindroth 1961-1969). Furthermore, the percent cover by exposed mineral soil is strongly correlated with the older burned stand in the RDA, supporting the speculation that drier conditions influence the carabid assemblages found there.

Differences were also observed between the older burned and clear-cut stands. Unlike assemblages of H53 stands, carabid assemblages of F58 stands are indistinguishable from control stand assemblages, suggesting that there is still time required before all old-growth species fully recover in these clear-cut stands post-harvest, which is similar to findings of other studies (e.g., Johansonn 2016). Furthermore, the tight clustering of carabid assemblages of H53 with H33 and H42 in the RDA suggests that carabid assemblages change much slowly in stands after ~30 years post-harvest, and the data at hand suggest no basis for projecting faster recovery during the following decades.

Catch of *L. ferruginosus*, a species associated with moderately moist, shaded ground (Lindroth 1961-1969), was notably caught in higher proportions in H53 than in F58 stands. This is perhaps surprising considering that F58 species assemblages were significantly correlated with increased ground cover of bryophytes, which are generally indicative of higher soil moisture (Lee and La Roi 1979). Further study is required to determine if *L. ferruginosus* will persist in harvested stands in the future, particularly as the habitat structure continues to change. Given differences between assemblages in H53 and F58, despite being relatively close in age, I cannot eliminate the possibility that recovery of some species depends on aspects of natural disturbance not effectively provided in harvested stands (e.g., Magura et al. 2001; Gandhi et al. 2004).

2.4.3 Correlation with ground vegetation

Variation in carabid catch and assemblage structure is influenced by microhabitat variation (Niemelä et al. 1996). Ground cover of mineral soil and nine plant taxa as well as basal area of white spruce (a likely proxy for degree of crown closure) and mountain alder were statistically correlated with the structure of carabid assemblages. Because local presence and relative abundance of plants reflect underlying abiotic conditions such as soil pH or sun exposure (Gough et al. 2000), plant composition in stands can reveal underlying abiotic conditions that might also influence carabid assemblages. For example, increased cover of graminoids was associated with the carabid assemblages of the youngest harvest stands (H12). Graminoids dominate most open habitats and are correlated with high exposure to sunlight and relatively low cover of trees or shrubs, as seen in H12 stands. These stands are also characterized by rich assemblages of carabids characteristic of open-habitat, such as *Amara*, *Harpalus* and some *Agonum* species, which are associated with exposed mineral soil (e.g., *Amara obesa* (Say); Cobb et al. 2007) or that feed on seeds of plants associated with disturbed sites (e.g., some *Harpalus* and some *Amara*, Brandmayr 1990). The H12 carabid assemblages are the only ones exhibiting correlations with such vegetation characteristics. Thus, the vegetation found at this point of succession is associated with a carabid assemblage structure that is locally unique amongst those of east slope pine stands.

Carabid assemblages in post-harvest clear-cuts (H19 stands) were statistically correlated with higher levels of wild blueberry, fireweed, and mountain alder. These correlations were also partly evident in burned stands of similar age (F17). However, F17 carabid assemblages overlapped in the RDA with the old-growth F110 stands, suggesting that they differed significantly from those in H19 stands (e.g., T. *chalybeus* and *M. arctica* were more common in

H19 than F17 whereas *S. haematopus* was commonly found in F110 and F17 but less so in H19). Differences observed between assemblages in burned and clear-cut stands of this age are consistent with results from other studies. For example, Buddle et al. (2006) showed that differences between aspen stands regenerating after burns and harvest persist for at least 20-30 years post-disturbance. Correlations between some plants and carabid assemblages in stands of this age (e.g. large cover of fireweed, blueberry and high basal area of mountain alder) suggest that assemblages are influenced by habitat conditions unique to this stage of succession.

Carabid assemblages of older harvested stands, H33, H44, and H53, cluster together and are commonly correlated with higher bunchberry cover, a plant species associated with lodgepole pine forests (Royer and Dickinson 2007). Nonetheless, these assemblages remain distinct in character of those from old-growth stands and they are also dissimilar from those in any of the burned stands. The oldest pyrogenic stands (F58 and F110) had higher cover of bryophytes and white spruce. Bryophytes are slow-growing, and commonly found in more stable conditions associated with older forests that take longer to establish and are home to characteristic species assemblages of arthropods (Kremen et al. 1993). Because F58 assemblages were correlated with bryophytes while those of H52 carabid assemblages were not, I suggest that moisture conditions may influence the difference in carabid assemblages between these groups of stands.

2.4.4 Implications for conservation

Forest managers attempt to conserve species sensitive to large scale harvesting by emulating aspects of natural disturbance. This involves large scale and long-term planning, such as leaving sufficiently large patches of old-growth on logged landscapes to serve as sources for recolonization (Hansen et al. 1991; Deans et al. 2003; Potvin and Bertrand 2004). In addition, there is evidence that increased retention of trees and CWD on logged stands has conservation value (Hautala et al. 2004; Work et al. 2004). Furthermore, special consideration is required for populations of less-mobile species that could become isolated and too small to persist given lack of linkage among habitats (e.g., Novák and Konvička 2006). Unharvested refuges of appropriate size may also serve to conserve species sensitive to climate change by buffering effects of changing climate that are most severe in areas without tree cover. Most of these considerations have been missing from large-scale forest exploitation based on clear-cutting operations but my study suggest that their adoption would likely support conservation of biodiversity of the native flora and fauna.

Nonetheless, even carefully planned harvests are unlikely to replace all aspects of fire (Gandhi et al. 2004). The question is: will it matter? The present study demonstrates that carabid assemblages recover significantly 52-54 years after clear-cut harvest, but that the recovery is not quite the same that has occurred in burned stands. Even carabid assemblages from F58 burned stands that closely resemble those in stands more than a century old lack some of the carabid species (*C. chamissonis, L. ferruginosus*) taken in some mature forest stands. Thus, more time may be needed for populations of such species to recover to pre-disturbance conditions, provided there are sources for re-colonization. Evidently, carabid assemblages in both burned and harvested stands on the eastern slopes are progressing toward generally similar end-points in terms of species richness and composition, and this is good news. Nonetheless, the present analysis suggests reasons for concern about persistence of mature forest species, such as *C. chamissonis*, on an actively managed landscape. Coupled with effects of climate change, landscape level reductions in populations of forest specialist species represent increased conservation risk.

	Harvested stands (H)					Burned stands (F)		
Age in 1989-90	-	-	5-12 y (H9)	15-21 y (H18)	28-30 y (H29)	-	-	80-90 y (F85)
Age in 2013-14	10-13 y (H12)	18-20 y (H19)	29-36 y (H33)	39-45 y (H42)	52-54 y (H53)	17 y (F17)	58 y (F58)	104-114 y (F110)
Stand 1 coordinates	53.25, -117.32	53.26, -117.47	53.19, -117.53[a]	53.21, -117.56[a]	53.23, -117.50[a]	53.22, -117.38	53.23, -117.37	53.25, -117.38[a]
Size (ha)	3.4	14.6	7.0	1.7	4.8B	11.9	18.9	4.8
Year of disturbance	2001	1996	1978	1969	1962	1997	1956	1910
Stand 2 coordinates	53.25, -117.32	53.25, -117.43	53.21, -117.56[a]	53.23, -117.49[a]	53.23, -117.50[a]	53.23, -117.37	53.22, -117.34	53.20, -117.54[a]
Size (ha)	12.0	12.4	20.0	2.0	3.6	2.3	20.8	5.2
Year of disturbance	2004	1994	1980	1975	1960	1997	1956	1900
Stand 3 coordinates	53.25, -117.32	53.26, -117.44	53.22, -117.55	53.22, -117.56	53.21, -117.49	53.25, -117.34	53.23, -117.35	53.20, -117.54
Size (ha)	7.3	18.3	7.5	9.5	4.3	18	10.0	3.9
Year of disturbance	2001	1994	1985	1970	1961	1997	1956	1900
Data based on 2013-14 samples								
Total catch	766	321	513	557	1267	393	1362	456
Trap-days [b]	2044	4032	4298	3794	4508	4074	4522	4242
Trap effort (%) [c]	6.5	12.8	13.6	12.0	14.3	12.9	14.4	13.5
Mean standardized catch rate ± SE [d]	369.7 ± 39.4 ^{A}	79.3 ± 4.5 ^{B}	118.5 ± 19.2 ^{B}	155.9 ± 39.1 ^{B}	278.7 ± 26.3 ^{AB}	94.6 ± 14.7	301 ± 160	104.2 ± 39.5 ^{B}
Observed species richness	31	27	13	17	20	26	13	16
Rarefied species richness ± 95%CI [e]	23.8 ± 3.1 ^{A}	36.4 ± 11.5 ^{A}	8.5 ± 1.5 ^{B}	11.7 ± 1.8 ^{B}	11.0 ± 0.7 ^{B}	25.2 ± 4.7 ^{A}	6.0 ± 0.5 ^{C}	11.7 ± 2.0 ^{B}

[a] denotes the stands which were sampled in both 1989-90 and 2013-14.
[b] one trap-day is defined as one trap in operation for one day.
[c] proportion of total trap-days for all stands combined.
[d] standardized to individuals per 1000 trap-days. Means followed by the same upper-case letter are not significantly different at alpha = 0.05 as determined by Tukey's test.
[e] coverage-based rarefaction extrapolated to 97.9% coverage. Means followed by the same upper-case letter are not significantly different (no overlap in 95% confidence intervals).
Note: Treatment labels (e.g. F110) denote disturbance types, harvest (H) and fire (F), followed by mean age of the replicate stands.

Table 1. Age, location and size of stands sampled in 1989-90 and 2013-14, and sampling effort, catch and species richness of carabids sampled in 2013-14. See Figure 1 for map of stand locations.

Species	**Catch**
Agonum cupreum Dejean	136
Agonum gratiosum (Mannerheim)* [b]	2
Agonum placidum (Say)	103
Agonum retractum LeConte [b]	3
Amara brunnea (Gyllenhal)*	2
Amara ellipsis (Casey)* [a]	1
Amara hyperborea Dejean [a]	2
Amara laevipennis Kirby [b]	20
Amara latior (Kirby)*	14
Amara littoralis Dejean*	19
Amara lunicollis Schiødte*	13
Amara obesa (Say)* [b]	3
Amara sinuosa (Casey)	7
Bembidion grapii Gyllenhal	66
Bembidion mutatum Gemminger & Harold* [b]	1
Calosoma frigidum Kirby* [b]	1
Carabus chamissonis Fischer von Waldheim	8
Carabus taedatus Fabricius	9
Calathus advena (LeConte)	1922
Calathus ingratus Dejean	1551
Cymindis unicolor Kirby	6
Harpalus fulvilabrus Mannerheim	19
Harpalus laticeps LeConte [b]	7
Harpalus megacephalus LeConte	25
Harpalus opacipennis (Haldemann)* [b]	3
Harpalus solitaris Dejean	67
Harpalus somnulentus Dejean* [b]	10
Leistus ferruginosus Mannerheim	24
Loricera pilicornis (Fabricius)* [a]	1
Miscodera arctica (Paykull)	29
Notiophilus borealis Harris*	9
Notiophilus directus Casey	11
Notiophilus semistriatus LeConte	8
Patrobus foveocollis (Eschscholtz)	71
Poecilus lucublandus (Say)* [b]	1
Pterostichus adstrictus Eschscholtz	249
Pterostichus pensylvanicus LeConte	26
Pterostichus riparius (Dejean)	49
Scaphinotus marginatus (Fischer von Waldheim)	361
Syntomus americanus (Dejean) [b]	28
Stereocerus haematopus (Dejean)	376
Synuchus impunctatus (Say)	207
Trichocellus cognatus (Gyllenhal) [a]	1
Trechus chalybeus Dejean	164
TOTAL	5635

* not caught in 1989-90

[a] caught only in 2013

[b] caught only in 2014

Table 2. Raw catch of each carabid species collected during 2013-14.

		Code (in RDA, Fig 3)	**RDA F value (ANOVA)**	**p-value**
Ground Vegetation/Soil (% cover)	Bryophytes	Bryo	17.1	0.001
	Cornus canadensis L.	Cncan	4.3	0.001
	Graminoids	Gram	5.2	0.002
	Fragaria virginiana Duchesne	Frvir	4.2	0.004
	Picea glauca Moench (saplings)	Pgsap	2.9	0.019
	Lathyrus ochroleucus Hook	Ltoch	5	0.001
	Vaccinium virgatum Aiton	Vcvir	2.5	0.030
	Chamaenerion angustifolium L.	Cmang	3.4	0.010
	Taraxacum officinale L.	Txoff	2.7	0.025
	Mineral soil	Soil	3.8	0.005
Trees/Shrubs (basal area)	*Picea glauca* Moench	Pcgla	2.7	0.034
	Alnus crispa Chaix	Alcri	2.6	0.037

Table 3. Summary of statistically significant vegetation and soil variables included in the RDA model (Figure 3).

Field season	**Mean monthly minimum (°C)**	**Mean daily minimum (°C)**	**Mean monthly maximum (°C)**	**Mean daily maximum (°C)**	**Mean monthly precipitation (mm)**
May-September (1989 and 1990)	-0.9 ± 3.3	4.7 ± 3.4	26.2 ± 2.4	17.9 ± 6.1	94.8 ± 44.7
May-September (2013 and 2014)	-3 ± 4.1	4.3 ± 4.2	28.4 ± 3.5	19.9 ± 6.2	63.8 ± 32.7
Δ between periods	-2.1 °C	-0.5 °C	+2.2 °C	+ 1.9 °C	-32.7 %

Table 4. Average (± standard deviation) monthly weather data (temperature and accumulated precipitation during the 1989-90 and 2013-14 field seasons (May-September). The last row shows percent change in means between 1989-90 and 2013-14.

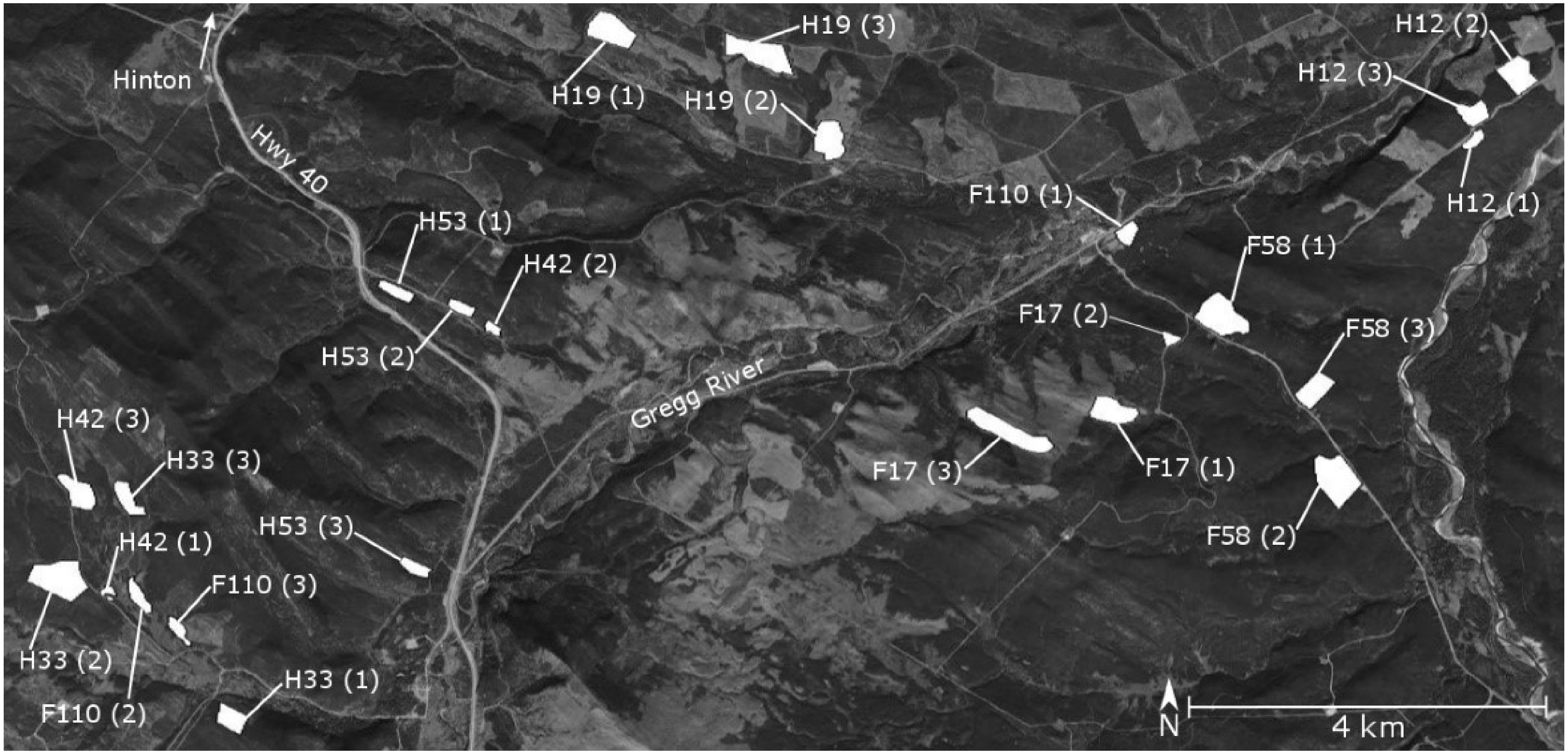


Figure 1. Map of the study area, 20 km south of Hinton in western Alberta. See Table 1 for details about each stand and explanation of the stand labels. The numbers in parentheses denote the assigned replicate number for each stand age class, Satellite image from Google Earth.

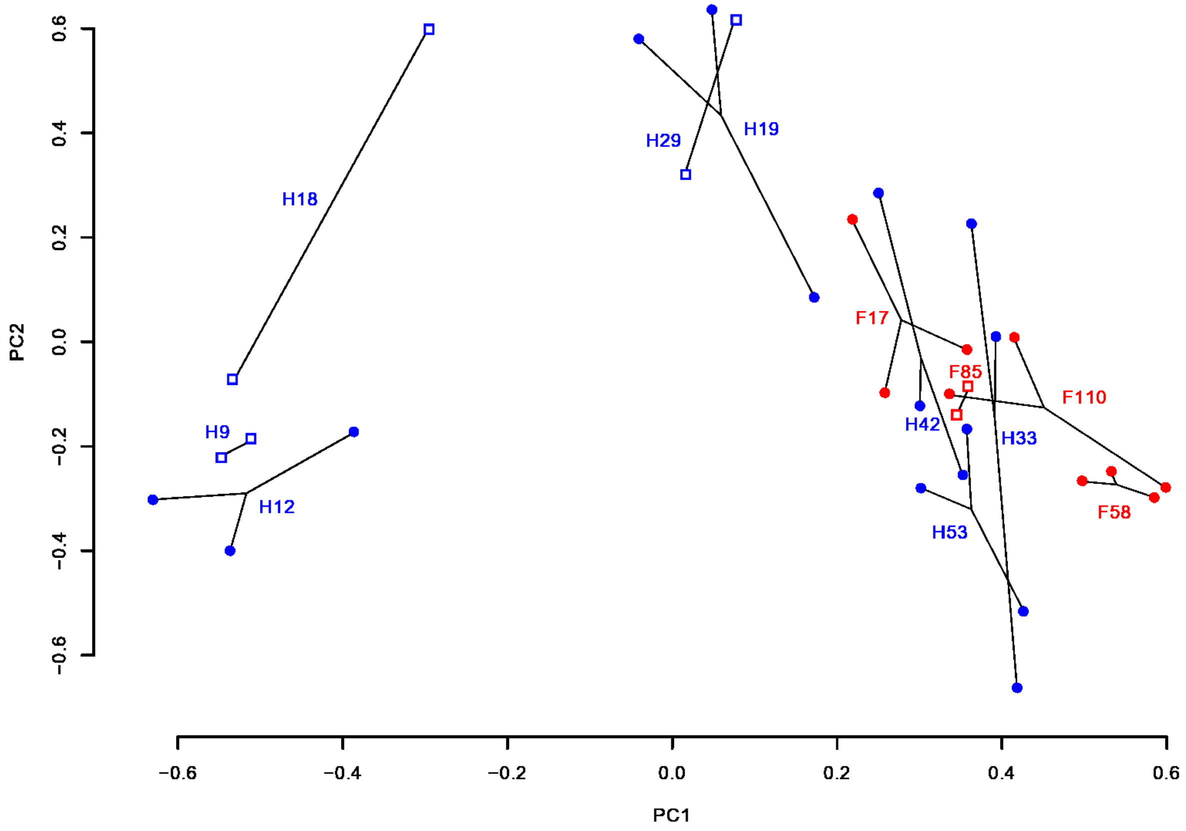


Figure 2. Principal Component Analysis of carabid assemblages sampled in harvested (H) and burned (F) stands in 1989-90 and 2013-14. Carabid standardized catches were Hellinger transformed before analysis. Open squares represent 1989-90 data and filled circles represent 2013-14 data; harvested stands are blue and burned stands are red. Lines connect replicate stands within each 'stand age × disturbance type' combination. Stand labels are defined in Table 1. The model was constructed using only data from harvested stands, and coordinates of burned stands were calculated from the PCA loadings on each species and plotted on the ordination.

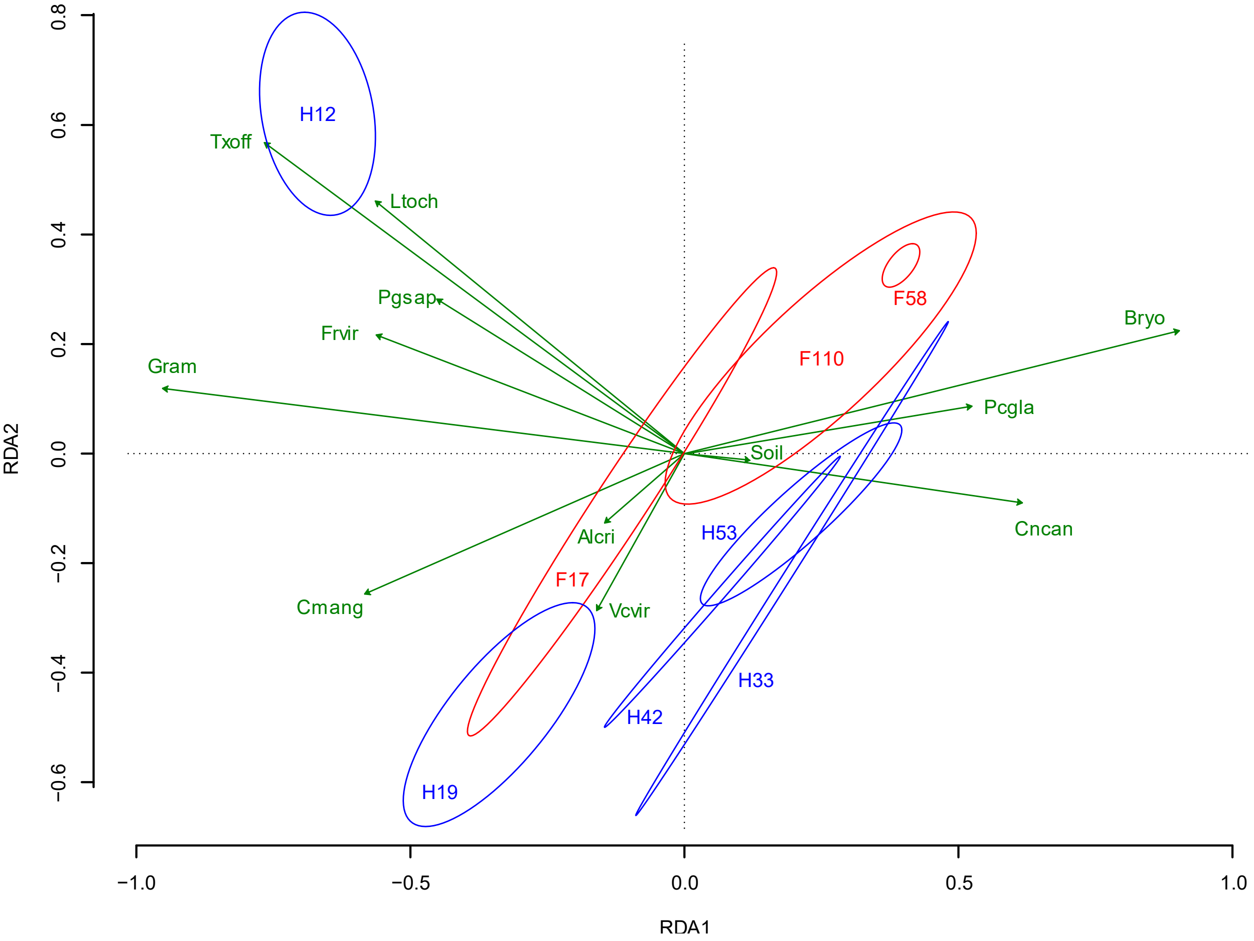
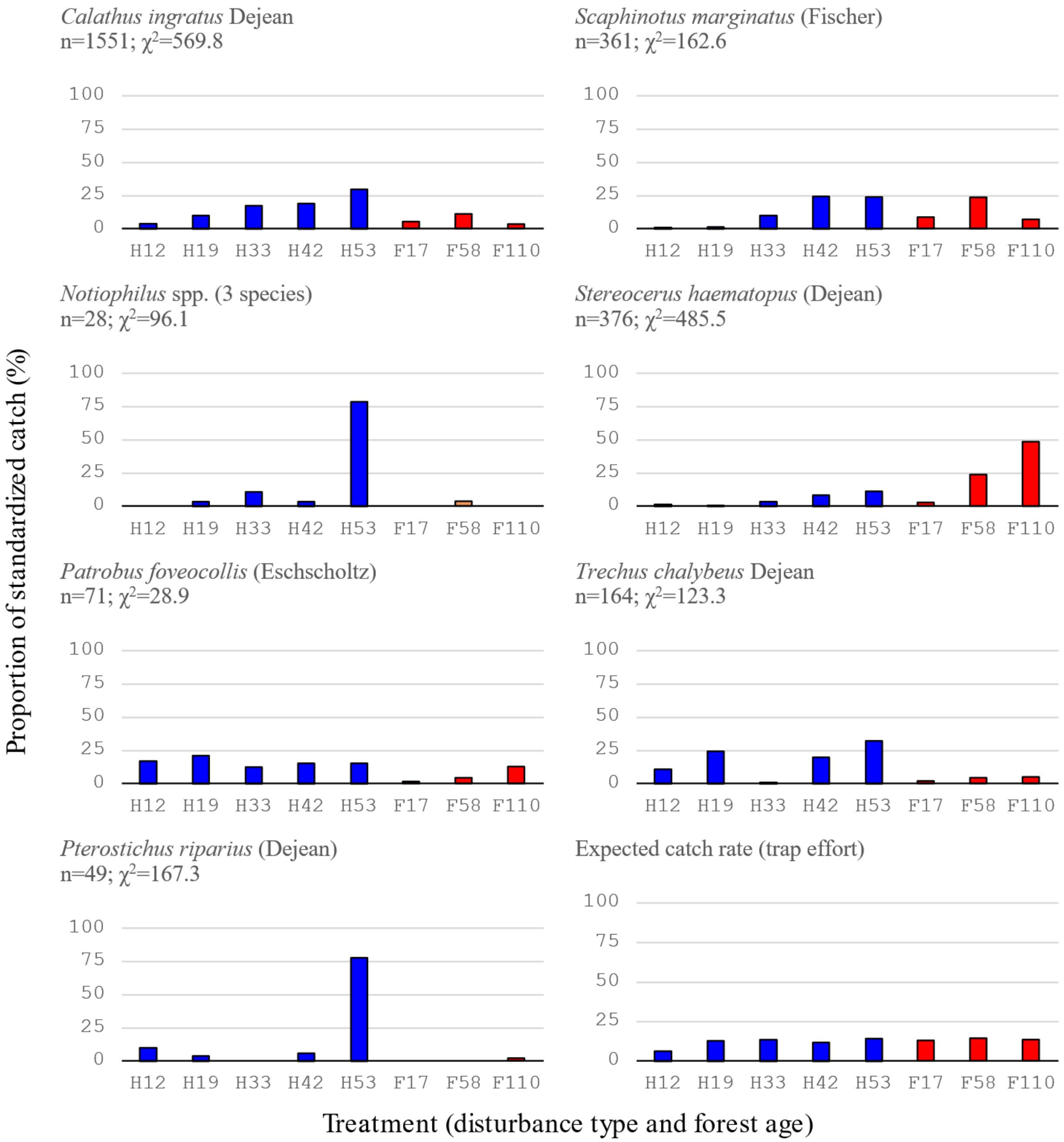


Figure 3. Redundancy analysis of carabid beetle assemblages in a chronosequence of harvested and burned stands sampled in 2013-14. Ellipses represent 95% confidence intervals for each ‘stand age × disturbance type’ combination based on Hellinger transformation of standardized catch data. Blue ellipses represent harvested treatments and red ellipses are burned treatments. Only statistically significant environmental (vegetation and soil) variables are depicted as green vectors on the RDA (see Table 3 for codes). Stand labels defined in Table 1.



Calathus ingratus Dejean
n=1551; χ^2=569.8

Scaphinotus marginatus (Fischer)
n=361; χ^2=162.6

Notiophilus spp. (3 species)
n=28; χ^2=96.1

Stereocerus haematopus (Dejean)
n=376; χ^2=485.5

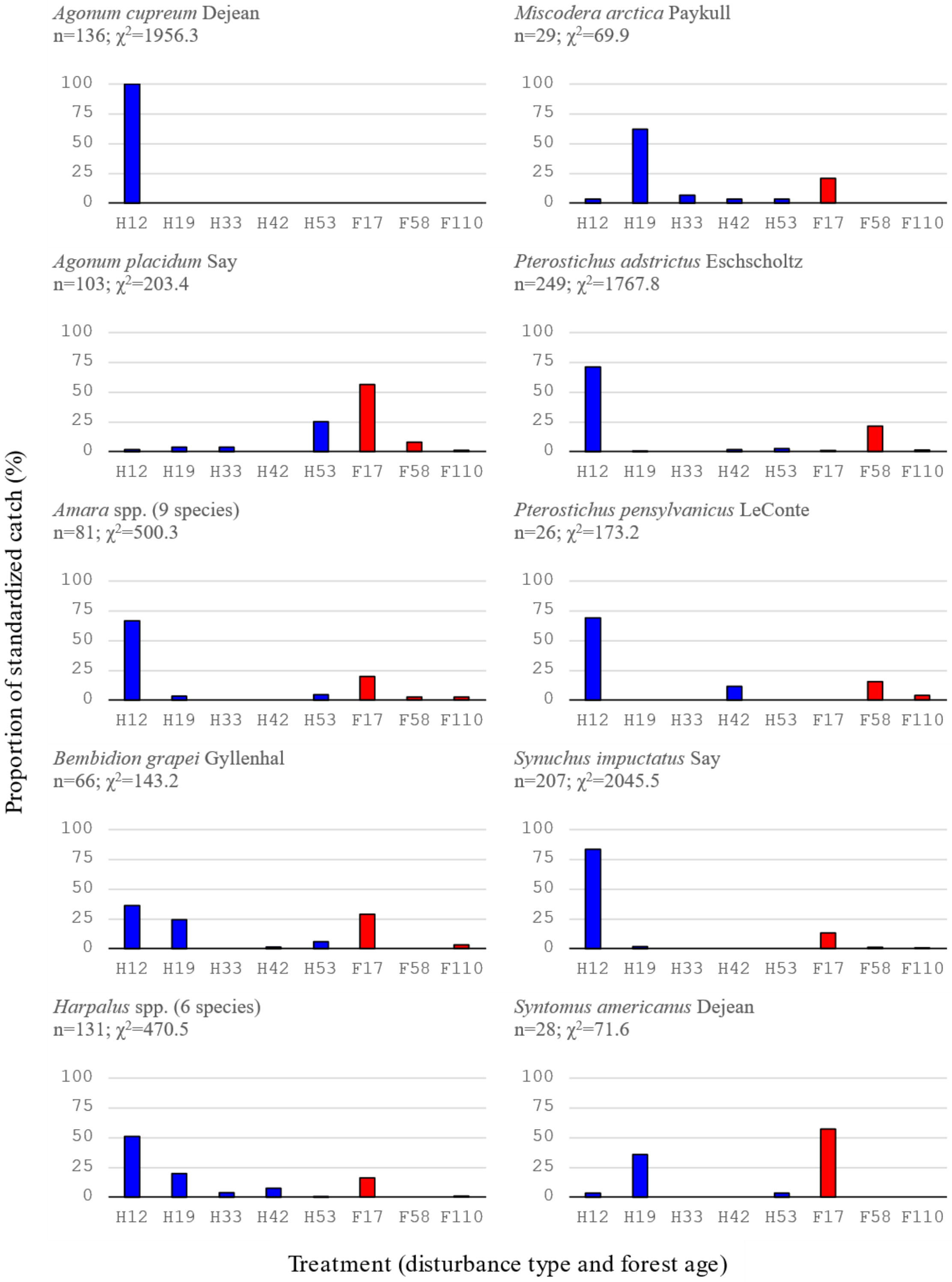
Patrobus foveocollis (Eschscholtz)
n=71; χ^2=28.9

Trechus chalybeus Dejean
n=164; χ^2=123.3

Pterostichus riparius (Dejean)
n=49; χ^2=167.3

Expected catch rate (trap effort)

Figure 4. Proportion of overall standardized catch of common generalist carabid beetle taxa (>15 individuals caught) in harvested (blue bars) and burned (red bars) stands. No taxa were evenly distributed across stand disturbance type and age combinations based on Chi-squared goodness of fit tests (χ^2 indicated above, df = 7, p < 0.001). Taxa that are evenly distributed on the landscape would be expected to be caught in proportion to trap effort (raw catch, n, given above). Expected catch proportions in evenly distributed populations on bottom right (stippled bars). See Table 1 for explanation of stand labels.



Agonum cupreum Dejean
n=136; χ^2=1956.3

Miscodera arctica Paykull
n=29; χ^2=69.9

Agonum placidum Say
n=103; χ^2=203.4

Pterostichus adstrictus Eschscholtz
n=249; χ^2=1767.8

Amara spp. (9 species)
n=81; χ^2=500.3

Pterostichus pensylvanicus LeConte
n=26; χ^2=173.2

Bembidion grapei Gyllenhal
n=66; χ^2=143.2

Synuchus impunctatus Say
n=207; χ^2=2045.5

Harpalus spp. (6 species)
n=131; χ^2=470.5

Syntomus americanus Dejean
n=28; χ^2=71.6

Figure 5. Proportion of overall standardized catch of common open habitat carabid beetle taxa (>15 individuals caught) that showed affinity for younger harvested (blue bars) and burned (red bars) stands. Chi-squared goodness of fit tests (χ^2, df = 7, $p < 0.05$) of raw catch (n) given. See Figure 4 (bottom right, stippled bars) for "Expected catch" proprtions for an evenly distributed population based on trap effort; see Table 1 for explanation of stand labels.

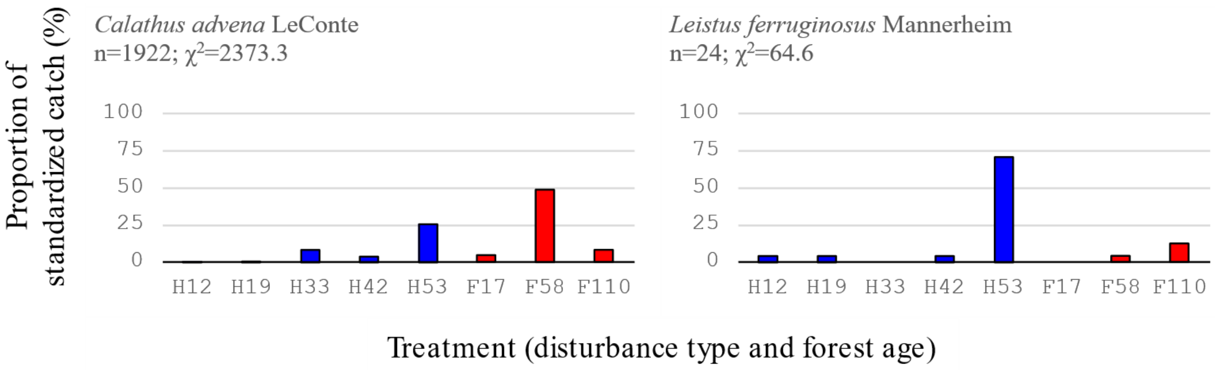


Figure 6. Proportion of overall standardized catch of common mature forest carabid beetle species (>15 individuals caught) that showed affinity for older harvested (blue bars) and burned (red bars) stands. Chi-squared goodness of fit tests (χ^2 df = 7, $p < 0.05$) of raw catch (n) given. See Figure 4 (bottom right, stippled bars) for “Expected catch” proprtions for an evenly distributed population based on trap effort; see Table 1 for explanation of stand labels.

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APPENDIX

		Minimum recorded temperature (°C)	Average daily minimum temperature (°C)	Maximum recorded temperature (°C)	Average daily maximum temperature (°C)	Monthly accumulated precipitation (mm)
1989	May	-3.1	1.0 ± 2.7	22.0	13.5 ± 5.0	61.3
	June	0.5	5.3 ± 2.4	26.6	19.2 ± 4.3	70.9
	July	3.4	7.5 ± 2.1	26.9	20.8 ± 4.1	110.0
	August	0.6	7.0 ± 3.0	26.3	17.5 ± 5.0	185.6
	September	-3.7	1.5 ± 2.0	23.7	16.7 ± 5.2	43.1
1990	May	-6.5	1.0 ± 3.0	23.9	12.9 ± 4.9	101.1
	June	1.4	5.6 ± 2.4	27.0	17.8 ± 4.6	94.6
	July	2.8	7.1 ± 2.5	30.0	20.6 ± 5.4	148.1
	August	0.1	7.8 ± 3.5	29.3	20.5 ± 6.0	85.0
	September	-4.0	2.7 ± 3.6	26.4	19.9 ± 4.3	48.6
2013	May	-8.5	1.0 ± 3.5	27.0	17.4 ± 4.5	77.0
	June	-1.4	5.1 ± 3.0	28.9	17.8 ± 4.3	106.9
	July	-0.6	6.7 ± 3.1	32.5	21.6 ± 4.8	116.7
	August	-0.9	6.6 ± 2.9	27.3	22.1 ± 3.1	42.8
	September	-3.7	2.8 ± 4.2	31.2	20.4 ± 6.5	9.4
2014	May	-11.2	0.0 ± 4.5	21.4	14.1 ± 5.4	50.6
	June	-2.1	4.2 ± 3.4	25.3	19.5 ± 4.1	84.0
	July	1.5	7.5 ± 2.7	32.5	25.7 ± 4.8	40.7
	August	1.3	7.1 ± 3.3	30.4	22.8 ± 5.3	63.7
	September	-4.3	2.1 ± 3.3	27.7	17.1 ± 6.9	46.5

Table A. Monthly weather data of field season during 1989-90 (1989, 1990) and 2013-14 (2013, 2014). Recorded by Alberta Climate Information Service (ACIS). The data represent township T049R24W5 (region of sample area, south of Hinton), estimated by interpolating data from the eight nearest weather stations (ACIS 2016).